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WHERE DOES ADAPTATION COME IN?¹

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To those—possibly imaginary—persons whose genetic interests are restricted to the mechanism of hereditary transmission, the problem of adaptation can have no great appeal, even if, for them, it exists at all. To others, again, whose sole interest in the organism is to analyze it as a physico-chemical machine, the question of the historical origin of this machine would seem to be a matter of quite minor importance. Some, indeed, have thought it reasonable to reject the whole notion of adaptation as anthropomorphic. In a symposium on this subject held by the American Society of Naturalists in 1912, one prominent participant expressed a view-point which, I doubt not, would still meet with approval in some quarters. This speaker relegated the conception of adaptation to the realm of the children's diseases of science—something which we would outgrow with advancing maturity. "It seems to be partly because biological problems are too complex for ready analysis at present," he tells us, "that the adaptational properties of living things are so often stated in terms other than those of the fundamental concepts of matter and energy."

Can you visualize a biological laboratory of the future in which everything observed by the investigator is to be "stated in terms of the fundamental concepts of matter and energy"? To many of us such a laboratory would

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be a very dull place indeed, and this even to those of us who recognize no element besides matter and energy as underlying biological phenomena.

There appear to be some biologists to whom "anthropomorphism" is the object of as great a phobia as was Soviet Russia to our more conservative fellow-citizens *before* the present realignment of forces in Europe. Anthropomorphic language is quite legitimate when we use it figuratively to avoid clumsy circumlocutions. It is vastly simpler, as well as vastly more sensible, to say that a bird, in the spring, builds her nest in order to raise her brood than it is to state that she goes through the process of nest-building by means of a series of catenary reflexes, initiated by gonadial hormones, and that the structure produced by her labors, if we may judge by previously observed cases, will probably be occupied by eggs which will develop, under proper temperature conditions, into young birds. We must insist, too, that the biologist who employs the former mode of expression is not in the least fooled by the words he uses. And if he adds that the bird has evolved "instincts" which are "adapted" to perpetuating the life of the species, surely no one but a pedant can object. We may grant that the situation so described requires further analysis.

Strictly speaking, every organism is adapted to the environment in which it lives; otherwise it would not be alive. In that sense, adaptation is coextensive with life, and the problem of the origin of adaptations is as inclusive as that of the evolution of life. More usually, however, the term is applied to cases in which adjustments of the organism to more specific features of the environment are discernible. These cases are particularly striking when the organism in question has adopted an environment quite different from that of its nearer relatives or its supposed ancestors. Here we may find obvious alterations of the original pattern which seem to bear very direct relations to needs imposed by the changed conditions of life. The fact that mistaken, even absurd, guesses have been made respecting the functional value of

some of the characters of organisms is no ground for dismissing the whole subject of adaptation as a topic for idle speculation.

I have, during much of my life, been particularly interested in adaptations relating to the concealment of animals from enemies or prey. This is preeminently a field in which both unbridled imagination and dogmatic denials have been much in evidence. But it is also a field in which some of the most striking and well-authenticated examples of adaptation are to be found. Doubt of the significance of these phenomena may take two forms. The most radical degree of skepticism is shown by those few who question the protective value of these color characters altogether, and strive to find for them a purely physical or chemical interpretation. Critics of a less skeptical turn of mind are ready to admit that at times an animal's color-scheme may be of value for protective or aggressive purposes, but they challenge us to show that such characters have been developed through natural selection because they confer these advantages upon the animal. The characters in question, they say, have a cause quite independent of the animal's need for concealment. The resemblance to surrounding objects is purely incidental.

It is curious that unfounded assertions such as these still continue to pass as arguments, although their fallacy has long been clearly evident to those familiar with the facts. I have devoted considerable space in several earlier papers to a refutation of some of these contentions,² and will discuss only a few points here.

If we had to do simply with a general color resemblance between an animal and its more familiar background, we might invoke some possible—even though utterly unproved—direct physical influence of this background upon the animal's skin. Thus we should be able to talk, as we are told a biologist should talk, "in terms of the fundamental concepts of matter and energy."

When, however, as often happens, an animal distributes

² AMERICAN NATURALIST, Vol. 69: 1935; *Proceedings of the National Academy of Sciences*, Vol. 20, 1934, and Vol. 21, 1935.

its pigment in significant patterns on the body surface and develops appendages on the skin, thus closely matching details of its usual habitat, another kind of vocabulary seems called for. Most of all, when the animal acquires a mechanism for color-change which is almost coextensive with the entire organism, involving as it does the eyes, large parts of the nervous system, highly specialized effector cells in the skin, and frequently the secretions of endocrine glands, and when, too, no function seems conceivable except that of rendering the organism inconspicuous against backgrounds of varying color and pattern, we seem forced to resort to a purely biological vocabulary and talk in terms of concealment from enemies or prey. I can not take time to discuss the experimental evidence which exists for the truth of this almost self-evident interpretation of the phenomena. I will only say that some of this evidence seems to me to be decisive.

Important light is being thrown upon both the physics and the chemistry of these processes of color change in animals, and we may hope that, in time, a fairly complete account of these may be written. Let us insist, however, that such an account will in no sense supersede, but will merely supplement, the biological account of these phenomena, which is a correct one so far as it goes.

How are we to explain the existence of such a mechanism as this on the basis of any one of the familiar evolutionary theories?

The Lamarckian hypothesis would explain it if this were otherwise admissible. The organism, according to this hypothesis, has striven to bring its appearance into harmony with that of its background. The results of each effort in that direction have been inherited in some measure by its offspring, and thus, in the course of many generations, the present marvelously efficient mechanism has been developed. This is a valid scientific hypothesis with no necessary taint of mysticism about it. It is an explanation, moreover, which has much *prima facie* probability. For it is a fact that many organisms can and do change their colors under the influence of the sense organs

and nervous system. (Whether we credit these animals with *effort* is a matter of small consequence.) Unfortunately, there is one serious, possibly fatal, obstacle in the way of accepting this type of explanation. I do not refer to our present inability to conceive of a probable mechanism through which the effects of functional activity can be inherited. That is not a fatal obstacle at all. I refer to the seeming total lack of convincing evidence that such a mode of inheritance exists. This last is a fact of much weight when we consider the intensive search for such evidence which has been carried on for many years. For the present, we seem forced to disregard Lamarckism as an explanation of the origin of adaptive mechanisms.

Thus, unless we are disposed to flirt with mysticism, or to accept purely verbal explanations of natural phenomena, there would seem left to us only one evolutionary hypothesis worth considering, that of natural selection. However, when we have said that, we have left some of the most important things unsaid. For we may, on the one hand, conceive of natural selection as acting continuously throughout the evolutionary process and accumulating small variations in the direction of fitness; or we may conceive of it merely as setting its stamp of approval upon a finished product. In the latter case, the role of natural selection is greatly restricted, and we must look elsewhere for the origin of adaptations. But if Lamarckism be ruled out, where shall we look? We all agree, I trust, that "inner perfecting tendencies" and the like do not belong in the realm of science.

Many of us had probably regarded the hypothesis of evolution through large, abrupt steps as having been finally disposed of. But its recent revival by one of our leading geneticists warrants giving it some serious attention. The subject has been discussed by many able biologists from Darwin down, and I shall merely review some of the considerations which seem to me to render this type of theory unacceptable.

My present discussion, let me repeat, relates to evolution through large, abrupt steps. Of course the query

arises forthwith: How large is "large"? Goldschmidt makes it plain that he has in mind the abrupt origin of the major categories of classification. He cites, at least without protest, the repetition by a recent paleontologist of St. Hilaire's well-known suggestion that the first bird may have emerged from the egg of a reptile. It may be recalled that the Dutch botanist Lotsy put forth, in 1916, somewhat similar views regarding the origin of the main subdivisions of the living world, offering as an example the probable sudden appearance of the vertebrate phylum through the hybridization of two invertebrates.

Such assumptions certainly avoid some of the difficulties inherent in the theory of selection as contemplated by Darwin, particularly the embarrassing scarcity of connecting links between major taxonomic groups, and the improbability that selection can act on the "pre-useful stages" of many organic structures. If none of these connecting links ever existed, we don't have to expect our paleontologists to find them; and if our main adaptive structures came into existence full-fledged and ready for use, we don't need to worry about pre-useful stages. These are such obvious advantages in the "saltatory" types of evolutionary theory that their proponents do not seem to be sufficiently impressed by their difficulties. But just in proportion as we conceive evolutionary steps to be great enough to avoid the difficulties just mentioned, are we forced to throw an impossible burden upon chance.

I don't know whether it is permissible, in the present advanced state of our knowledge, to quote such a back-number as Charles Darwin, but my temptation in this case is strong. "He who believes that some ancient form was transformed suddenly through an internal force or tendency into, for instance, one furnished with wings, will be almost compelled to assume, in opposition to all analogy, that many individuals varied simultaneously. . . . He will further be compelled to believe that many structures beautifully adapted to all the other parts of the same creature and to the surrounding conditions have been suddenly produced; and of such complex and wonderful co-

adaptations, he will not be able to assign a shadow of an explanation. . . . To admit all this is, as it seems to me, to enter into the realms of miracle, and to leave those of Science." Thus spoke Darwin!

To the saltatory evolutionist, our newly acquired lung or wing or plumage is supposed to have arisen, as a functioning entity, through a single "macromutation." In so far as he splits up these changes into smaller steps and envisages a cumulative process, he is departing from his original thesis and losing some of the advantages gained by his special type of theory. Bear in mind that none of these new acquisitions is merely a homogeneous mass of living matter, to be influenced in a "more" or "less" direction by mutation. Each is a complex, integrated structure, the success of which is altogether dependent upon the simultaneous modification of a large variety of tissues. Add to this the necessary coincident modification of other parts of the organism already present. Indeed, where we have to do with a radical change in the animal's life, as from an aquatic to a terrestrial mode of existence, there may be hardly a single part of the body which will not need revision.

Those who have perused the writings of Herbert Spencer—if any such persons remain—will recall that the existence on every hand of these "coadaptations" of structure and of function furnished him with one of his strongest lines of argument for the Lamarckian factor in evolution. It must be admitted that this hypothesis, if otherwise tenable, would provide us with a beautifully simple explanation of the facts.

Spencer's argument for the "inadequacy of natural selection," in this case, rested upon the improbability that the necessary variations in all these functionally related parts would occur simultaneously. I think we must admit that this argument is quite valid if we have in mind variations large enough to bring about considerable changes in the bodily machinery. If, on the other hand, we have in mind variations of small magnitude, of a size comparable with many of the mutations best known to

modern geneticists, the progressive variations in the several organ systems would not have to occur simultaneously. This was pointed out by Wallace in a reply to Spencer. The wide range of mutual adjustability of the various parts of the body during development would prevent serious disharmonies. Selection must be supposed to act upon the entire organism, not upon single characters. (Least of all—to bring our discussion up to date—does it commonly act upon single genes.) One individual doubtless profits by one set of advantages, another by another. All these characters, in a freely interbreeding population, may, however, be ultimately incorporated into the heritage of the species.

It seems obvious that any one who sponsors a theory of evolution by large steps must provide an agency through which functionally related parts are brought to vary together in such a way as to insure the harmonious cooperation of the parts affected. That neither genetic linkage nor the manifold effects of single genes affords a mechanism for such correlation, to more than a very limited extent, will probably be readily granted. It is probable that such an agency, if it exists, must be sought in the field of developmental physiology rather than that of genetics.

In his important recent volume on "The Material Basis of Evolution," Dr. Goldschmidt has discussed at considerable length various aspects of the physiology of growth and development. He stresses such facts as the changes in the relative size of parts which frequently result from a general increase or decrease of body size and the radical effects upon body structure of accelerations of the rate of growth. Of some of these cases, he writes that "a simple shift in the velocity of one of the integrating processes relative to the others will account for the primary change with all the later unavoidable consequences during subsequent development." Much is made by Goldschmidt of the effects of such drugs as thyroxin which hasten metamorphosis and thus give the appearance of initiating profound morphological and physiolog-

ical changes. "Feeding with thyroid makes the axolotl transform into the *Ambystoma*, a transformation which involves an immense morphogenetic change from gills to lungs, with all the concomitant changes in all systems of the body." On the other hand, the permanently gilled *Perennibranchiata* remain throughout life in the axolotl stage and experiment has shown that they can not be made to metamorphose: "they are genetically unfit for complete metamorphosis."

Goldschmidt puts aside as irrelevant the "problem as to whether the perennibranchiates are phylogenetically primitive or whether they are derived as neotenic larval forms from metamorphosing Amphibia. The point of our argumentation," he says, "is independent of such speculations. The facts demonstrate that there are Amphibia in which a hereditary norm of reaction permits metamorphosis, which is a morphological change of an order of magnitude characteristic of the taxonomic difference between families or orders."

I have quoted Professor Goldschmidt at some length because it seems to me that these passages illustrate a fundamental fallacy in his evolutionary argument. From the standpoint of evolution, there is really a vast difference between the induction of metamorphosis in a secondarily larval form like the adult axolotl, whose ancestors undoubtedly lost their gills at maturity, and the induction of similar far-reaching changes in forms whose ancestors may never have led a terrestrial existence. That attempts to effect such transformations in the latter group of amphibia have failed is not surprising. If they had succeeded, should we not merely have rather strong evidence that they too are neotenic larvae like the axolotl?

Goldschmidt has surely marshalled a highly interesting set of facts along the lines indicated. But before accepting his deductions from these facts, we must await the discovery of a case which he has not yet presented. This would be a case in which the hormonally induced remodelling of an organism has resulted in the appearance of a set of adaptive structures new to its ancestral his-

tory. It is easy to demonstrate that a single genetic change may bring about the total loss of a number of complex structures. But this throws no light whatever on the processes through which these structures arose in evolutionary history. A person seeking information on the manufacture of watches would not be much enlightened by learning that one of these instruments could be demolished by a single blow of a hammer. As little can we draw valid conclusions concerning racial history from the experimental restoration of a structure formerly present but now suppressed under the usual conditions of life.

If we admit the preceding contentions, we must also admit that all these interesting facts relating to norms of reactivity, seasonal dimorphism, endocrine control, homoecosis, neotenic larvae, rudimentation, etc., while vastly important as contributions to our knowledge of ontogeny, have little bearing upon the mechanism of evolution.

In the present state of our knowledge, we seem driven to the rather banal conclusion that evolutionary change has resulted mainly from the accumulation through selection of small genetic differences. This is a return to Darwinism in the narrower sense of that word, though such an avowal does not imply the admission that nothing has been learned in this field since Darwin's time.

Where adaptations are of a very general sort, such as increased fecundity, resistance to disease or ability to withstand the rigors of climate, there is little difficulty in conceiving of the operations of the evolutionary process. It is but natural that recent geneticists, in citing hypothetical cases in which one mutant type is supposed to have an advantage over another, appear to have had in mind adaptations of this general type.

That some character of dubious value to the organism may be genetically correlated with an elementary advantage, say fecundity, and thus be carried along like a rider on an appropriation bill, is no novel idea, as some may have supposed, but was suggested by Darwin himself in the "Origin." It is perhaps characters of the "rider"

type which chiefly distinguish subspecies from one another. It is difficult to imagine specific adaptation to local conditions in the differing lengths of the bodily appendages of mammals and birds inhabiting different geographic areas. Or perhaps, as some have averred, adaptation has played no part, even indirectly, in the origin of such characters. It may be that the mutant genes involved in their production have gained local ascendancy through the vicissitudes of chance, operating in small populations.

At the opposite pole from the simple adaptational characters last discussed are those complex mechanisms involving the cooperation of a number of important organ systems. Here belong, for example, such cases as the mechanism of color change to which I referred at some length earlier. To Darwin, the processes by which such complicated machinery came into being were simply an extension of those which led to the minor differences between one species or variety and another, namely, variation, inheritance and the differential survival of strains displaying the advantageous characters in a higher degree.

Any such passage in evolutionary history is conceivable, as already insisted, only if we recognize its gradualness. To begin with, this adaptive mechanism did not arise *ex nihilo*. It was built upon an antecedent foundation of nervous and other elements acquired early in the ancestral history of the vertebrate stock. And throughout the entire period of its development, this faculty must have shown quantitative differences in its degree of perfection. That individual differences in the capacity for chromatic adaptation exist between members of the same species is a familiar fact to those who have experimented in this field. It may be fairly assumed, too, that these differences are in part genetic. Presumably multiple factors have been concerned in a large way. On the basis of all analogy, this is a faculty which we should be able to improve greatly by means of artificial selection. That

natural selection has been operative in the present case is rendered doubly probable by experimental proof that the faculty in question may be of life-saving importance.

Unfortunately, acceptance of this account of the origin of adaptive characters through natural selection has been retarded by the prevalence of inadequate notions regarding the role played by mutation. Much has been said of the occasional appearance of mutant genes which give to their possessors some particular advantage. Such advantageous genes have been presumed to be gradually accumulated through selection until they become established in the germplasm of the species. Mutation and selection go hand-in-hand, it would seem, in every evolutionary advance.

In reply to this, as it seems to me misleading, account of the case, I will quote from an earlier discussion which I published some years ago. Let me repeat my disclaimer of any originality in the views here expressed.

It is hardly necessary to point out that selection is not concerned, directly, with single genes, but with the aggregate fitness of entire organisms, and that this fitness commonly depends upon a large number of varying genetic elements. Unlike the more or less pure cultures which are frequently reared in the laboratory, natural populations are genetically highly mixed. This condition is maintained through the free interbreeding of diverse strains, probably, in extreme cases, through the crossing of widely different races or even species. Thus, while every one of the underlying unitary differences may be supposed to have originated, at some time, as a single mutation, the material upon which selection acts has arisen through the endless shuffling of these elements as a result of sexual reproduction. The processes of mutation and selection thus need not go on *pari passu*. Much genetic change might come about, and be widely disseminated throughout a population, before it became subject to selection at all. Large genetic differences might thus be available at the very commencement of a given selective process, and the gap between the "pre-useful" and the "useful" stages of a structure might be bridged by purely fortuitous gametic combinations.³

In writing those words, I had in mind no such large-scale remodeling of organic structure as would be called for by a truly saltatory theory of evolution. I had in mind such truth as may deservedly be credited to the notion of "pre-adaptation."

³ *Bibliographia Genetica*, Vol. 9, 1932.

UTILIZATION OF SPERM BY THE FEMALE *DROSOPHILA MELANOGASTER*

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In various experiments with *Drosophila melanogaster* it is desirable to know what fraction of the spermatozoa transferred in copulation is utilized by the female in fertilizing her eggs. To secure this information it is necessary to determine the approximate number of sperms transferred per copulation as well as the total output of fertile eggs by the inseminated female. Such information has been obtained and is here presented. Some effort has also been made to determine whether sperms stored in the seminal receptacles may take precedence over subsequently deposited sperm in fertilizing the eggs.

The authors have had considerable aid in collecting the data here presented, and wish to thank Margaret Hoover Brooks, Ruth Bate Eckardt, Jean Lane, Taylor Hinton, Berwind N. Kaufmann and Carl B. Kaufmann.

NUMBER AND UTILIZATION OF SPERMS TRANSFERRED IN A SINGLE COPULATION

Determination of the approximate number of sperms transferred by the male during copulation has been made by direct count, using wild-type Swedish-b flies. Other efforts to appraise the number of sperms by employing dilution methods similar to those used for counting blood cells of the higher animals were discarded as unreliable after trials by individuals experienced in that type of analysis.

Females dissected immediately after mating usually show in the vagina the recently deposited spermatozoa aggregated in a more or less spherical mass. By application of a fixative, this sperm clump may be coagulated *in situ*, and in a few minutes when sufficiently hardened may be removed as a unit. It seems quite probable that some loss of peripheral sperms occurs by their migration

to the seminal receptacles prior to the time of fixation, and some additional loss as the material is passed through the various reagents used in preparing it for study. Such losses, however, appear to remove only a small fraction of the total mass, the major portion of which is retained for microscopical examination.

The sperms were stained by the Feulgen method so that the heads alone would be colored, since the deposition of pigment in the long tails following the use of acetocarmine and the basic dyes so obscures the picture that an accurate count of the number of cells can not be made. Considerable difficulty was experienced in securing uniformly good Feulgen preparation of this material even in batches receiving the same type of treatment at the same time. For this reason it was not always possible to obtain counts from consecutive matings of the same male.

The actual counts of numbers of sperms secured from four females after copulating with previously unmated six-day-old males were as follows: 3,877 (♂ 2, a); 3,793 (♂ 3, a); 3,593 (♂ 1, a); 3,215 (♂ 5, a). From two males which copulated a second time immediately following the first, sperm counts of 2,518 (♂ 5, b) and 1,390 (♂ 8, b) were obtained. From third consecutive matings, counts of 2,618 (♂ 17, c); 1,996 (♂ 5, c) and 989 (♂ 18, c) were recorded, and from a fourth consecutive mating a single count of 1,047 (♂ 5, d). In the case of male number 5, counts were secured following four consecutive matings during a four-hour period. As indicated above these were 3,215, 2,518, 1,996 and 1,047.

The percentage of fertile eggs was determined by comparing the number deposited with the number hatching. In order to collect these data, each of eleven males was permitted to copulate with three virgin females during a four-hour period. Each female was given a number in our records corresponding to the number of the male with which she had mated, and a letter A, B or C indicating the sequence of mating. Following copulation each female was isolated in a vial containing a tray of yeasted food on which eggs might be deposited. Fresh food was

provided daily during the egg-laying period. A record was made of the number of eggs deposited during each 24 hours, and the food was then set aside for subsequent inspection to determine the number of larvae, pupae and adults. Throughout the experiment flies were kept at room temperature that ranged between 20 and 22 degrees C.

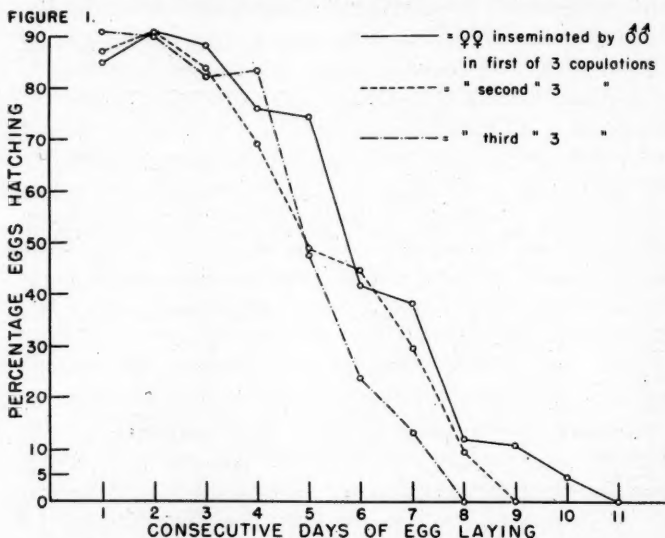
Results of the A, B and C matings are presented in summarized form in Table 1, and shown graphically in Fig. 1. The numbers of eggs laid by all the females of each of the three groups have been totaled on the basis of the number of the day of laying, irrespective of whether these

Table 1. DAY-BY-DAY CHANGE IN FERTILITY OF EGGS LAID BY Sw-b ♀♀ FOLLOWING A SINGLE INSEMINATION

Successive matings by same male		CONSECUTIVE DAYS OF EGG-LAYING									
		1		2		3		4		5	
		L	H	L	H	L	H	L	H	L	H
A	No.	141	120	232	212	261	231	308	234	210	156
	%	85.10±3.00		91.38±1.84		88.51±1.97		75.97±2.44		74.29±3.02	
B	No.	141	123	201	183	238	200	278	192	230	113
	%	87.23±2.81		91.04±2.01		84.03±2.37		69.06±2.77		49.13±3.30	
C	No.	114	104	136	123	142	117	158	132	166	79
	%	91.23±2.65		90.44±2.52		82.39±3.20		83.54±2.95		47.59±3.88	
Successive matings by same male		DAYS OF EGG-LAYING CONTINUED									
		6		7		8		9		10	
		L	H	L	H	L	H	L	H	L	H
A	No.	167	67	85	28	77	9	47	5	24	1
	%	41.61±3.88		32.94±5.10		11.69±3.66		10.64±4.50		4.17±4.08	
B	No.	213	95	95	28	85	8	41	0	50	0
	%	44.60±3.41		29.47±4.68		9.41±3.17					
C	No.	56	13	31	4	26	0	20	0	7	0
	%	23.21±5.64		12.90±6.02							

Comparison of numbers of eggs laid (L) with number hatching (H) for a 10-day laying period. Groups A, B, C each include several ♀♀. Each female mated only once. Those in group A were inseminated by Sw-b ♂♂ during first of three consecutive copulations; those in B by the second of these copulations; those in C by the third.

represented consecutive calendar days. Thus all eggs deposited by the eleven females of the A group on the first day of laying have been totaled regardless of whether the eggs were deposited on the day of mating or on a subsequent day. This procedure has been adopted because in the course of the egg-laying period individual females may permit 24 to 48 hours to elapse without depositing any eggs. Apparently no decrease in the efficacy of the sperms in fertilizing eggs is occasioned thereby, since Muller (1940) has reported that sperm still functions after being stored by the female as long as 30 days.



Not all the tested females continued to lay throughout the ten-day period represented in Table 1, so that the totals in each group through the later days of the series are for a diminishing number of individuals. The most extended laying period of any individual terminated within 15 calendar days of the time of mating. Only one female laid any fertile eggs after the twelfth day, and these were but 9 in number. Considered in terms of egg-laying days, no fertile eggs were deposited after the tenth day. The greatest number of eggs laid by any female of

the A group during this period was 322, of the B group 288 and of the C group 215. The largest number of larvae hatching from eggs laid by any member of the A group was 204, of the B group 156 and of the C group 204.

The highest degree of fertility (about 91 per cent.) was attained in all groups on the second day of laying. Failure of 9 per cent. of the eggs to hatch may be due in part to failure of fertilization but is more probably attributable to sterility factors in the Swedish-b stock causing death of the embryos. In support of the latter of these alternatives there is the evidence obtained by cytological study of 99 of the first-laid eggs of an inseminated female which indicated that 98 had been fertilized (Demerec and Kaufmann, 1941), even though in that experiment the sperm had been subjected to 5,000 roentgens of x-radiation.

Groups A and B gave somewhat lower percentages of fertile eggs for the first day of laying than for the second. The values are attributable to exceptional females in each group which deposited a high percentage of eggs that failed to hatch. Presumably these eggs were unfertilized, although the females had been supplied with abundant sperm as testified by the fact that on the second day of laying both showed percentages of fertility greater than the average for the group.

Following the second day of laying, there was a consistent decline in fertility, which terminated with the deposition of only sterile eggs. No fertile eggs were laid after the tenth day by any female of group A, or after the eighth day by any female of group B or after the seventh day by any female of group C. The differences in the three groups are probably attributable to the reduced quantity of sperm transferred in the later matings of a series as compared with the earlier ones.

These data suggest, therefore, that a considerable mass of sperm must be available in the seminal receptacles if all or nearly all the eggs passing through the uterus are to be fertilized. During the first two laying days, when presumably nearly all eggs have been fertilized, the mean

number deposited is about 15 to 22 per cent. of the individual's output for the entire egg-laying period (36 of 239 for the group A female; 23 of 165 for the group B female; 43 of 194 for the group C female). Individual females, however, show considerable variability. Thus, one female of group A deposited about 60 per cent. of her eggs (186 of 318) before fertility dropped below 92 per cent. Such variability confuses any effort to estimate the total amount of sperm that must be present to ensure fertilization of all eggs. Another complication is the inability to determine the total number of sperms a given individual receives in copulation. In the face of such data it can only be pointed out that about the first fifth or sixth of the eggs deposited following a single insemination have all been fertilized, and that among succeeding fractions there is a gradually decreasing probability that an egg will receive any sperm.

Comparison of the number of sperms delivered during copulation with the total number of eggs fertilized indicates that the average female utilized about 20 to 30 sperms per fertilized egg (*ca* 4,000/137 for group A; *ca* 3,000/100 for group B; *ca* 2,500/128 for group C). A considerable portion of these sperms enter some of the eggs as supernumeraries, since polyspermy occurs in *Drosophila*. Huettner (1924) has reported that occasionally more than 30 spermatozoa may be found in the egg of *D. melanogaster*. In the experience of one of the authors (B. P. K.) numbers in excess of 7 to 8 per egg are rarely encountered in sectioned material. It would seem therefore that large numbers of sperms are squandered during the laying of the first eggs, and that the low fertility among the eggs laid subsequently is attributable to this wastage. Further evidence on this point might be secured by a cytological study of the numbers of sperms found in eggs selected on successive days during the egg-laying period.

The evidence here obtained by using untreated flies indicates therefore that fertility decreases as the number of sperms available is reduced during successive days of

Table 2. DAY-BY-DAY CHANGE IN FERTILITY OF EGGS LAID BY SW-b QQ FOLLOWING A SINGLE INSEMINATION BY X-RAYED (3000r) SW-b ♂♂

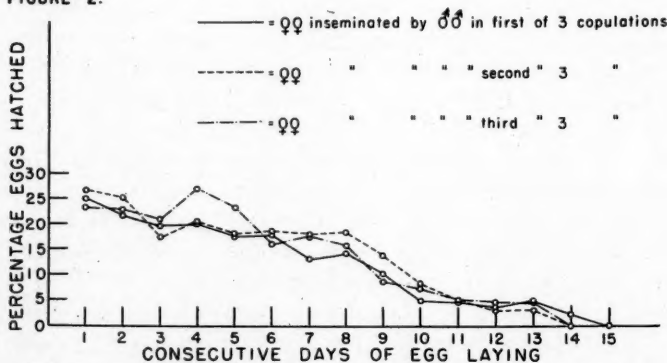
SUCCESSIVE MATINGS BY SAME MALE		CONSECUTIVE DAYS OF EGG-LAYING																	
		1	2	3	4	5	6	7	8										
A	No.	847	212	947	207	877	172	1004	202	748	130	901	160	1051	138	683	97		
	%	25.03 ± 1.49	21.86 ± 1.34	19.61 ± 1.34	20.12 ± 1.26	17.38 ± 1.39	17.76 ± 1.27	13.13 ± 1.04	14.20 ± 1.33										
B	No.	819	220	767	193	656	114	767	157	715	130	743	138	857	155	416	76		
	%	26.86 ± 1.55	25.16 ± 1.57	17.38 ± 1.48	20.47 ± 1.46	18.18 ± 1.44	18.57 ± 1.43	18.09 ± 1.32	18.27 ± 1.89										
C	No.	519	122	529	121	506	106	607	164	438	102	463	74	505	90	229	36		
	%	23.51 ± 1.86	22.87 ± 1.82	20.95 ± 1.81	27.02 ± 1.80	23.29 ± 2.02	15.98 ± 1.70	17.82 ± 1.70	15.72 ± 2.41										
SUCCESSIVE MATINGS BY SAME MALE		DAYS OF EGG-LAYING CONTINUED																	
		9	10	11	12	13	14	15	16										
A	No.	474	48	291	14	432	20	367	13	287	14	177	4	75	0	42	0		
	%	10.13 ± 1.39	4.81 ± 1.25	4.63 ± 1.01	3.54 ± 0.96	4.88 ± 1.27	2.26 ± 1.12												
B	No.	357	49	269	22	185	9	261	8	209	6	87	0	54	1				
	%	13.73 ± 1.82	8.18 ± 1.67	4.86 ± 1.58	3.07 ± 1.07	2.87 ± 1.11													
C	No.	151	13	159	12	142	7	65	3	22	1	8	0						
	%	8.61 ± 2.28	7.55 ± 2.10	4.93 ± 1.82	4.62 ± 2.60	4.55 ± 4.44													

L = Number eggs laid; H = Number hatching.

egg laying. A similar conclusion was reached concerning the sharp reduction in fertility which was sometimes obtained when the female was mated with an irradiated male that had just completed several other copulations (Demerec and Kaufmann, 1941). In those experiments fertility was low from the start as a consequence of the dominant lethals induced by 3,000 roentgens of x-radiation. Since the percentage of dominant lethals should not vary greatly in successive matings if sperms are being tested that were mature at the time of treatment, a comparison of the fertility of eggs laid on successive days during this period should give a measure of the percentage of eggs fertilized.

When such a comparison is made it is found that there is also a gradual decrease in fertility during the latter part of the egg-laying period. The data presented in Table 2 and Fig. 2 are from *series A* of our previous

FIGURE 2.



study and include the counts of eggs laid by females which had been mated with irradiated males on the day of treatment. Forty-one males were used in this experiment and each was permitted to mate with 3 virgin females. The combined data for the first, for the second and for the third consecutive matings are represented in the three curves of Fig. 2.

BEHAVIOR OF SPERMS DELIVERED TO A SINGLE FEMALE
IN SUCCESSIVE COPULATIONS

The efficacy of sperms transferred in later copulations in taking precedence in fertilizing eggs over sperm previously deposited can be measured by using stocks carrying suitable genetic markers. Experiments by Nonidez (1920) in which wild-type and Bar males were mated successively with wild-type females suggested that the sperm from the Bar males used in the second mating could mix with any residue of the wild-type remaining in the ventral receptacle. From the limited data supplied by 7 females, Nonidez noted that if the ventral receptacle were emptied prior to the second insemination, the eggs deposited during the next few days produced only Bar females. The subsequent appearance of wild-type as well as Bar females suggested that wild-type sperm stored in the spermathecae from the first mating were also being used. Similar experiments conducted by Nachtsheim (1927) on three species of *Drosophila*, *melanogaster*, *simulans* and *pseudoobscura*, were likewise interpreted as indicating that in general the introduction of the second type of sperm caused cessation of production of offspring of the first male, which might reappear, however, as the progeny of the second mating became fewer and fewer. Dubinin (1928) from extensive data obtained from *D. melanogaster* and *D. obscura* reached the conclusion that the newly deposited spermatozoa completely eliminate the type previously deposited. On the other hand, Lobashov (1939), using various stocks of *melanogaster* decided that after double copulation a complete mixture of sperm occurs in the receptacles. Polyandry also occurs frequently in the grouse locusts, and Nabours (1927) has noted that in *Paratettix texanus* the last male or males copulating with the female tend to become the parents of the predominant proportion of her offspring. Beliaiev's observations on the silkworm (1937), according to Lobashov, likewise indicate that in this species a mixture of sperms from the different fathers may take place.

Lobashov's paper was particularly interesting because

it contained the suggestion that subsequent to the mixing of the sperm, elimination of the type of lowest viability might occur, so that selective fertilization would ensue. In certain of his experiments he tested sperm of various wild-type stocks (Florida, Samara, Bukhara) in combination with those of *sc v f car* and white males in their ability to fertilize eggs of *sc v f car* females, and found that the sperms carrying the recessive genes accounted for a much smaller proportion of the total offspring when the *sc v f car* or white males were used initially than when used subsequent to the wild-type. These facts suggested to Lobashov that elimination of sperms occurs and that mortality was considerably higher in the *sc v f car* and white than in the wild-type. One aspect of this problem of differential survival has been considered by Nachtsheim and by Muller and Settles (1927). These workers had shown that in *D. melanogaster* longevity of sperm is not dependent on its genetic constitution. Nachtsheim had suggested that probably the life cycle of this species is too short to detect such differences in viability of sperm types, although an objection to this view may be found in the discovery of Muller and Settles that sperm which had been kept in the female for three months at 10 degrees C. was viable in part. At the time that Lobashov's article came to our attention we had begun similar experiments, the results of which are here presented.

In the first of these studies, 24 plexus brown speck females were mated singly in vials with *px bw sp* males. Copulation was observed and occurred in every case within the first 3 hours. The males were then removed without anesthetizing, and the following day each female was placed in a vial with 4 to 5 brown males. Subsequently wild-type (Oregon-R) and Lobe^s males were used. No effort was made to observe copulation with the *bw*, wild-type or *L* males, since they were permitted to remain with the females either 24 or 48 hours (the time was varied in different matings). The females remained in each vial for about 48 hours, and were then transferred to

fresh food. Counts were made of the different types of offspring hatching in these vials.

Judging by the types of offspring, the 24 females mated at least 62 times. One of the 24 gave only one type of offspring; 10 gave two types; 11 gave three; and 2 gave all four. Although copulation with *px bw sp* males was observed in all cases, 8 of the 24 females failed to produce *px bw sp* offspring. It has been shown that sperm transfer is not necessarily a concomitant of copulation, and these cases may fall into that category, or they may have involved the transfer of only very small quantities of sperm which could easily be displaced, as seems possible from some of our other data.

Measurements of displacement can be made when progeny have been produced following the earlier as well as the later matings. Thus, from the eggs laid in the first vial by one female there were obtained 20 *px bw sp* offspring, from the second vial of the series 7 *px bw sp* and 8 *L* flies, and from the next eight vials 81 *L*. When flies of two kinds appeared in the vial in which the second type of male had been placed, it was not always possible to determine whether the different types of offspring appeared concurrently as a result of the mixture of the two kinds of sperms in the receptacles of the female, or whether, as in the case mentioned, the 7 *px bw sp* flies came from eggs deposited by the female prior to insemination by the *L* male. It is clear, however, that the sperm carrying *L* had completely displaced any residue of *px bw sp* remaining after the fertilization of about 27 eggs. A similar behavior was shown by 6 additional females which produced two types of offspring. Other females showed that the second type of sperm utilized can likewise be displaced by a third type.

Although, in the cases cited, replacement was complete so that there was no recurrence in later transfers of types of offspring which had appeared first, this sequence does not hold invariably. For example, the *bw* offspring from one female appeared in the second and third vials, were absent from the fourth to the ninth, but reappeared in the

tenth. Comparable behavior was shown by 4 other females. Certain other females produced two types of offspring over several days, revealing thereby that a mixture of different sperm types may occur.

From this preliminary survey it was apparent that the method of utilization of different sperm types following successive inseminations could vary with the individual female. Relatively small numbers of *px bw sp* and *bw* offspring were obtained as compared with the wild-type and *L* and this suggested that selective fertilization might be occurring. In this connection it seemed desirable to determine more accurately to what extent actual mixing of different kinds of sperms might be taking place in the receptacles. For these reasons another set of experiments was conducted, again using *px bw sp* females but varying in all possible ways the sequences in which *px bw sp*, wild-type (Oregon-R) and Curly/Glazed males were made available for mating. The latter were substituted for the *L* males, because of greater ease of identification of the mutant characters.

Females were permitted to remain with each type of male for 72 hours, and no effort was made to observe copulation. Replacement of males and transfers to vials containing fresh food were made as in the previous experiment without anesthetization. The different kinds of progeny obtained from these vials are shown in Tables 3 to 8. Females which furnished only one type of offspring are placed first, separated by a double line from those which produced two types, and followed by those giving the three possible types. When several females furnished the same types of offspring in the same sequence they were grouped as shown in the vertical column under the caption "Number of ♀♀." Each horizontal line shows the number and types of flies obtained in the order of their appearance. By means of day-to-day counts as the flies emerged an effort was made to determine whether different types appearing in the same vial arose from the deposition of the different kinds of eggs concurrently or in succession. When the same kinds of

TABLE 3.

Succession of ♂♂
Time available
for each mating—
72 hrs.

		27 px bw sp ♀♀							
		TYPES OF OFFSPRING IN SEQUENCE							
	Number of ♀♀	+	Cy or Gl	+	+	+	px bw sp	Cy or Gl; px bw sp	Cy or Gl
				Cy or Gl	px bw sp				
+; Cy/Gl; px bw sp	9	616							
	5	254	301						
	1	33					2		
	1	151		39; 5					
	2	297			43; 9				
	1	45			34; 25				
	1	35		15; 15		24			
	1	34			8; 9	1			
	1	57		28; 9					122
	1	31		1; 17					11
	2	143			48; 27		24		
	1	56		25; 1				68; 14	
	1	74	100	14; 4				2; 1	4
TOTALS		1826	401	122; 51	133; 70	25	26	77; 15	137

offspring appeared on several consecutive days, it could be assumed that a mixture of the different types of sperms had occurred in the receptacles. Combinations of offspring produced under these conditions are listed in italics so that they may be distinguished from other similar combinations which could have been produced if the first type of sperm used had been entirely displaced by another type (see, for example, in Table 7 the two groups, one of 9, the other of 4 females which produced *px bw sp*, then *px bw sp* and wild-type, and finally only wild-type offspring).

The number of females tested in the entire experiment was 188. The total number of matings recorded was 362, of which 113 were with wild-type, 113 with *Cy/Gl* and 116 with *px bw sp* males. The average number of matings per female was 1.93, with the range in the 6 series

TABLE 4.

Succession of ♂♂
Time available
for each mating—
72 hrs.

		28 px bw sp ♀♀							
		TYPES OF OFFSPRING IN SEQUENCE							
	Number of ♀♀	+	px bw sp	+	+	+	+	+	
				Cy or Gl	px bw sp		px bw sp; Cy or Gl	Cy or Gl	
+; px bw sp; Cy/Gl	7	671							
	1								86
	3		15						
	2	193							136
	3	38			42; 22				
	1	28			37; 13	7			
	4	302		85; 74					261
	1	122		48; 38					59
	3	116			32; 59				201
	1	27			2; 1				78
	1	81					59; 1; 1		
	1	34					12; 21; 7		94
TOTALS		1612	15	133; 112	113; 95	7	71; 22; 8		915

TABLE 5.

TABLE 5.		32 px bw sp ♀♀									
Succession of ♂♂		TYPES OF OFFSPRING IN SEQUENCE									
Time available for each mating- 72 hrs.		Number of ♀♀	Cy or Gl	Cy or Gl; +	+	Cy or Gl	Cy or Gl; +; px bw sp	+	px bw sp	+	Cy or Gl; px bw sp
Cy/Gl; +; px bw sp		12	1618								
		2	142	140; 104							
		1	138	1; 1							
		1	214								
		1			1						
		1			78	9					
		1	39	82; 29	23						
		4	484	109; 6		329					
		1	37	3; 3	2	1					
		2	103	106; 168						41	
		1	63	25; 40	81					31	
		1	111	33; 126	11			10; 20			
	1	76	100; 127				3; 33	19			
	1	155	18; 66	14			16; 18		39		
	1	175	86; 38								
	1	28	29; 28				1; 4			1; 12	
	1	32	131; 29			4; 7; 9	3; 4			1; 20	
TOTALS		3415	863; 765	210	339	4; 7; 9	33; 79	125	39	2; 32	

covering the rather narrow limits between 1.74 and 2.09. Of the 188 females, 55 mated with only one type of male, 92 with two of the three types available, and the remaining 41 with all three. These counts have been based on the types of offspring observed, and do not take into consideration the possibility of complete displacement of sperm prior to its utilization, nor the additional possibility that successive matings with males of the same genetic constitution may occur.

The total number of offspring obtained was 27,887, of which about 40 per cent. were wild-type, 46 per cent.

TABLE 6.

TABLE 6.		32 px bw sp ♀♀									
Succession of ♂♂ Time available for each mating- 72 hrs.		Number of ♀♀	TYPES OF OFFSPRING IN SEQUENCE								+
			Cy or Gl	px bw sp	Cy or Gl; px bw sp	px bw sp	Cy or Gl	Cy or Gl; +	px bw sp; +	Cy or Gl; px bw sp; +	
Cy/Gl; px bw sp; +	7	941									
	1		14								
	1	91		1; 1							
	3	303		123; 96	83						
	1	22	2								
	3	193								13	
	1	134		1; 1		5					
	4	437					96; 126			91	
	1		20					10; 13		58	
	1		44		12; 13	49	1				
	2	143		102; 77	31					97	
	3	156		60; 44						83	
	1	110		20; 11		153	1; 1				
	1	90		22; 66	46			20; 22			
	1	70		65; 56				10; 12		94	
	1	59		82; 34		2			17; 6; 49	100	
TOTALS		2749	80	488; 393	209	161	97; 127	40; 47	17; 6; 49	536	

TABLE 7.
Succession of ♂♂
Time available
for each mating—
72 hrs.

		35 px bw sp ♀♀							
		TYPES OF OFFSPRING IN SEQUENCE							
	Number of ♀♀	px bw sp	px bw sp; +	+	px bw sp; +	px bw sp; Cy or Gl	px bw sp; +; Cy or Gl	Cy or Gl	+; Cy or Gl
		px bw sp	px bw sp; +	+	px bw sp; +	px bw sp; Cy or Gl	px bw sp; +; Cy or Gl	Cy or Gl	+; Cy or Gl
px bw sp; +; Cy/Gl	7	75							
	2	46	39; 154						
	2	30	34; 19						
	1	8		60					
	9	192	103; 402	1078					
	4	129	136; 313	99					
	1		23; 57	83					
	1		10; 66	82					
	1	18	37; 144	32	1; 37				
	2	121				14; 38		225	
	1	47						41	
	1	30	66; 84				3; 1; 2	271	
	1	5	33; 19	38			1; 28; 2	154	2; 13
	1	90	11; 1			5; 32		203	1; 1
	1		20; 24	31				81	7; 88
TOTALS		791	512; 1283	1503	1; 37	19; 70	4; 29; 4	975	10; 102

either *Cy* or *Gl*, and only about 14 per cent. *px bw sp*. These figures are not strictly comparable, since fewer virgin females were available to the wild-type males than to the other types (55 as compared with 64 for the *Cy/Gl* and 70 for the *px bw sp*) and since a given type of mating with virgin females accounts for a larger proportion of the progeny than if it is used subsequent to other matings. Such factors may be responsible for the greater numbers of *Cy* and *Gl* flies than of wild-type, but can not account for the dearth of *px bw sp*, because males of that type not only had the largest number of females with which to mate but also accounted for a larger number of matings than the other kinds of males.

Detailed information concerning this disparity is fur-

TABLE 8.
Succession of ♂♂
Time available
for each mating—
72 hrs.

		34 px bw sp ♀♀							
		TYPES OF OFFSPRING IN SEQUENCE							
	Number of ♀♀	px bw sp	px bw sp; Cy or Gl	Cy or Gl	+	px bw sp; +	+	px bw sp; Cy or Gl	Cy or Gl
		px bw sp	px bw sp; Cy or Gl	Cy or Gl	+	px bw sp; +	+	px bw sp; Cy or Gl	Cy or Gl
px bw sp; +; Cy/Gl	8	188							
	1	15		1					
	4	68	80; 101	299					
	3	154							
	3	236				18; 89	440		
	1	34				4; 93	107		
	1	25	12; 49	65				1; 13	
	1			72	56; 21				
	1			59	28; 1		127		
	2	38	81; 75		117; 68				
	5	80	123; 180	165	202; 429		227		
	2	46	89; 36	73	39; 175		16		
	2	61	63; 185		20; 82		170		
TOTALS		945	448; 626	734	462; 876	22; 182	1314	1; 13	17

nished in Tables 3 to 8. The numbers and percentages of the different types of offspring in the different mating sequences are presented in Table 9. Counts of progeny obtained from all females are listed in the first three columns, those from females that mated with at least the first two kinds of males provided are presented in the next three columns, and in the last three columns are the data obtained from those females that mated with all three types of males. The two latter groups, from which females that mated only once are excluded, give a some-

TABLE 9. FREQUENCIES OF DIFFERENT TYPES OF OFFSPRING *px bw sp* ♀♀

Sequence of mating	All ♀♀, whether mating 1, 2 or 3 times			Only ♀♀ mating with at least first 2 types of ♂♂ furnished			Only ♀♀ mating with all 3 types of ♂♂ furnished		
	+	<i>Cy</i> or <i>Gl</i>	<i>px bw sp</i>	+	<i>Cy</i> or <i>Gl</i>	<i>px bw sp</i>	+	<i>Cy</i> or <i>Gl</i>	<i>px bw sp</i>
+; <i>Cy/Gl</i> ; <i>px bw sp</i>	No. 2106	666	111	804	666	15	169	186	15
	% 73.0	23.1	3.9	54.1	44.8	1.0	45.7	50.3	4.1
+; <i>px bw sp</i> ; <i>Cy/Gl</i>	No. 1936	1035	132	515	381	117	363	381	82
	% 62.4	33.4	4.3	50.8	37.6	11.5	43.9	46.1	9.9
<i>Cy/Gl</i> ; +; <i>px bw sp</i>	No. 1054	4623	245	1054	3005	245	807	1277	245
	% 17.8	78.1	4.1	24.5	69.8	5.7	34.7	54.8	10.5
<i>Cy/Gl</i> ; <i>px bw sp</i> ; +	No. 759	3512	728	458	1845	684	458	1152	395
	% 15.2	70.3	14.6	15.3	61.8	22.9	22.8	57.5	19.7
<i>px bw sp</i> ; +; <i>Cy/Gl</i>	No. 2862	1151	1327	2862	847	1070	236	847	264
	% 53.6	21.6	24.9	59.9	17.7	22.4	17.5	62.9	19.6
<i>px bw sp</i> ; <i>Cy/Gl</i> ; +	No. 2372	1852	1416	1267	1620	782	1267	1092	581
	% 42.1	32.8	25.1	34.5	44.2	21.3	43.1	37.1	19.8
TOTALS	No. 11089	12839	3959	6960	8364	2913	3300	4935	1582
	% 39.8	46.0	14.2	38.2	45.9	16.0	33.6	50.3	16.1
GRAND TOTALS	27887			18237			9817		

what better measure than does the first group of competitive ability in the different sequences.

From these data it is evident that either the wild-type or the *Cy/Gl* males when used initially contribute the sperm which fertilizes the major portion of the eggs developing into adult flies. On the contrary, the *px bw sp* males used in the same relative position in the mating series, account for one-fourth or less of the total progeny. The same general disparity between *Cy* or *Gl* and wild-type on the one hand, and *px bw sp* on the other is apparent when males of these kinds are used for the second or third matings of the series. Differences between *Cy* and *Gl* and wild-type are less pronounced, although the for-

mer is the numerically superior group. When the frequencies in those sequences in which wild-type followed *Cy/Gl* are compared with those in which *Cy/Gl* followed wild-type, employing the *t* test as a measure of the significance of the means (using data derived from those females that mated at least twice) a value of *P* of about 0.5 is obtained. It thus appears that chance alone might give the observed distribution even if equality were to be expected in larger samples. But, as will be shown subsequently, there is some evidence that offspring having *Cy* or *Gl* chromosomes survive better in competition than those carrying the wild-type chromosomes (cf. Ward, 1923), and this may account for the numerical superiority recorded.

In the light of these findings it becomes important to determine whether the small number of *px bw sp* flies is attributable to inadequacies of mating and sperm transfer, to low viability of the sperm so that selective fertilization occurs, or to poor viability of the homozygous *px bw sp* embryos and larvae.

The large number of matings by *px bw sp* males (116) indicates that they are not inhibited by any structural or physiological handicaps from copulating with the *px bw sp* females. In order to determine whether transfer of an adequate quantity of sperm was effected, two counts were made of sperm masses which had been dissected from females immediately after copulation. The numbers of individual sperms recorded were 2,012 and 1,731. Although these values are somewhat lower than those for the first copulation of wild-type males reported earlier in this paper, they are within the range obtained for the second and third successive copulations. The quantity of sperm should be adequate, therefore, to guarantee fertilization of a large number of eggs, since, according to the data presented in Table 1, the females do not deposit many less fertilized eggs following second and third copulations than following the first.

Despite what appears to be an adequate sperm supply, the average number of flies per mating derived from *px*

bw sp by *px bw sp* was very low, only 34.1 (3,959/116) as compared with 98.1 (11,089/113) for the *px bw sp* by wild-type, and 113.6 (12,839/113) for *px bw sp* by *Cy/Gl*. In order to determine whether this disparity was occasioned by poor viability of the zygotes, or by larval competition, counts were made of the numbers of adults emerging from equal numbers of eggs of three kinds, those fertilized by *px bw sp*, those by wild-type and those by *Cy/Gl* sperm. Batches of about 50 eggs of each kind were collected on spoons and transferred to half-pint milk bottles containing yeasted food. Several such bottles were prepared so that 1,060 eggs of each kind were placed in competition. From them there emerged 928 wild-type, 821 *Cy* and *Gl* and 603 *px bw sp* flies. It seemed therefore that the small percentage of *px bw sp* flies in these cultures (25.6 per cent. of those hatching) might be referable to poorer viability of the homozygous recessive stock.

Additional tests were therefore run to determine the numbers of the various kinds of offspring when females inseminated by the different types of males were permitted to lay their eggs in the same bottle. Several bottles were prepared, each containing three such females whose copulations had been observed. Since no effort was made to control the number of eggs laid in the bottle, the type of competition approached more closely that which might follow multiple insemination, except that no mixture of sperm types was possible and there could thus be no differential fertilization. From these cultures there were obtained 1,191 wild-type (36.8 per cent.), 1,529 *Cy* and *Gl* (47 per cent.) and 521 *px bw sp* flies (16.1 per cent.). The ratio of the three types is approximately 1 *px bw sp*: 2.3 wild-type: 3 *Cy* and *Gl*. These proportions are similar to those which were found among the total progeny of the various mating sequences, as shown at the bottom of Table 9. Moreover, a similar proportion is found among the various types of progeny provided by the first matings of those females that had all three types of offspring. In the two series of matings in which wild-type males were used first, 44.5 per cent. of all offspring

were wild-type; in the series in which *Cy/Gl* males were used first, 57 per cent. of the offspring were *Cy* or *Gl*; but when *px bw sp* males were used first, only 19.5 per cent. of the progeny were *px bw sp*. Similar data obtained from the three middle columns of Table 9 likewise give a ratio of about 1 *px bw sp*: 2.3 wild-type: 3 *Cy* and *Gl*. Ratios among flies obtained from eggs fertilized by sperms contributed in the second or third matings are not always in such close agreement. In the two series in which *px bw sp* was used for the initial mating, the *Cy* or *Gl* and wild-type flies were found in the ratio of 1.29:1 as compared with 1.28:1 for the controls. But when wild-type males were used first, the *Cy* or *Gl* flies were 5.85 times as frequent as *px bw sp*, as compared with a ratio of 2.94:1 in the controls. In one of these series more *Cy* and *Gl* flies were found than might be expected on the basis of relative viability, whereas in the other there was a preponderance of *px bw sp*. Such contrary results are not easily harmonized with the assumption that differential fertilization might have occurred, but seem rather to be attributable to variability occasioned to a large extent by the small number of flies secured from those crosses in which the females mated with all types of males provided. In the light of these comparisons, particularly those involving the total progeny and those obtained from the initial matings, it seems that the disparity in numbers among the different types of offspring is attributable to their relative viabilities rather than to any selective fertilization which might result from physiological advantages possessed by one type of sperm over another.

DISCUSSION

Many genetic experiments involving offspring of males of *Drosophila* treated with x-rays have been conducted on the assumption that any selected group of progeny derived from such males furnishes a random sample of the treated spermatozoa. We have found, however, that considerable variability may occur in different experiments given identical treatments, or even among different

samples from the same treatment. Since the variability in these cases could not be attributed to errors of measurement, or to the existing culture conditions, it was apparently biological in nature. Accordingly, an effort was made to measure some of the determinable factors involved in mating and egg-laying, such as the quantity of sperm transferred in successive copulations and the utilization of this sperm by the female in fertilizing her eggs.

Certain aspects of these problems were treated in our previous study (Demerec and Kaufmann, 1941). It was shown that irradiated males that mated repeatedly soon exhausted the supply of mature sperm available for transfer, as evidenced by the fact that no fertile eggs were deposited by females with which they copulated later in the day. Before exhausting the available supply, a considerable number of sperms may be transferred; our counts show 8,776 from a single male in four successive copulations within four hours. Acknowledging some loss due to the technique employed, it seems probable that this male had 10,000 or more mature sperms available for transfer. This estimate is no measure, however, of the total number of sperms present in the testis of the adult male of *D. melanogaster*. Males which have exhausted the supply of available sperm on one day may again copulate and transfer sperm on the succeeding day, as was shown in our previous study. Several workers have also noted that the testis of the adult male of this species is nearly filled with spermatozoa, and the present authors have shown that despite repeated copulations sperm which was mature at the time of x-ray treatment was not exhausted during the next twelve days. The statement that the two testes contain 8,000 to 10,000 completed spermatozoa, attributed to the senior author by Auerbach (1941) as an oral communication transmitted through Dr. P. Ch. Koller, can refer only to the number which a male can transmit in a few successive copulations and not to the total number present. Failure to transfer sperm in the later matings of a series may indicate that sperms

have not moved close enough to the vas deferens to permit ejaculation, or may be attributable to the inactivity of the ejaculatory apparatus, as Duncan (1930) has suggested in an attempt to explain the inability of old males to transfer sperm in copulation from testes filled with mature cells.

In our previous study it was shown that there was considerable variability in the proportions of fertile and sterile eggs laid by different females, and it was suggested that if only a small quantity of sperm were transferred it might prove insufficient to guarantee fertilization of all eggs. This interpretation, based on total egg counts extending over several days, finds support in the data presented in Table 2 of the present paper, showing the day-to-day output of fertile and sterile eggs by those females that utilized sperm transferred in one of the first three successive matings accomplished by males immediately following their irradiation. The curves obtained from these counts (Fig. 2) show unequivocally that as the supply of sperm is depleted a gradually decreasing proportion of eggs is fertilized. Data obtained from untreated males (Fig. 1 and Table 1) indicate a similar decline in fertility accompanying diminution of the quantity of sperm available.

These findings indicate that a considerable amount of sperm must be present in the receptacles if all eggs passing through the vagina are to be fertilized. It is not possible to define this minimum quantity except in the very general terms that the original mass of sperms ensures fertilization of about the first fifth of the eggs laid by the average female. Since polyspermy may occur in *Drosophila*, the supernumerary sperms penetrating the egg will help to deplete the store in the receptacles. Additional loss may be occasioned by the release of sperms which fail to enter the micropyle. If passage of the egg through the vagina should be accompanied by relaxation of the muscles controlling the openings of the ducts of the receptacles, it would be expected that the number of sperms released and the chances of penetrating the micro-

pyle would be greatest when abundant sperm is present immediately following insemination. As the supply diminished there would be a lessened probability that any sperm would enter the egg.

Such factors may account to a large extent for the apparent replacement in some crosses of one type of sperm by another. Abundant evidence is presented in Tables 3 to 8 that intermixing of sperms deposited in successive copulations may occur. If a small quantity of sperm residual from an earlier mating should become mixed with a more abundant supply subsequently deposited, it would be expected that the latter would on a chance basis provide the individual sperms fertilizing most of the eggs. This may be the explanation of the type of replacement reported by Nonidez and Nachtsheim, for these workers allowed 6 to 8 days to elapse before providing the second type of male with which the female could copulate. Since an appreciable reduction of the sperm supply need not entail the laying of large numbers of eggs, the apparent displacement of one type of sperm by another may follow the deposition of only a few fertile eggs. And if the quantity of sperm originally transferred in copulation should be small, the effect mentioned would be heightened. Some of the cases shown in Tables 3 to 8 may be interpreted in this way.

Somewhat more difficult to interpret are the results obtained from such crosses as occurred in our preliminary experiment, in which *px bw sp* females copulated with *px bw sp* males but failed to produce offspring showing these characters. It has been suggested that little or no sperm may have been released in these copulations, and this seems the more plausible explanation, despite the fact that 4- to 5-day-old males were used that had not previously mated. The alternative explanation that a considerable mass of sperm was transferred in these matings would require the effective displacement of the *px bw sp* sperm by a type subsequently deposited, as Dubinin believed invariably occurred. Under such con-

ditions the second type of sperm would need to displace sperm from receptacles already well filled. Nonidez was the first to show that in this situation a mixture of the two types of sperms is the more likely probability. Such an interpretation is supported by the data shown in Tables 3 to 8. The possibility that the culture conditions in our preliminary experiment were unfavorable for the development of *px bw sp* embryos seems ruled out by the production of individuals of this genotype in the majority of the matings.

In the light of these considerations it would appear that chance fertilization by one of the available sperms, coupled with differential viability of the embryos, is sufficient to account for the different frequencies obtained following different mating sequences. Such an interpretation makes superfluous the assumption of selective fertilization. Lobashov, however, has concluded that selective fertilization does occur because sperms carrying certain recessive genes are eliminated. To cite one of his experiments, *sc v f car* females, mated with both Florida (wild-type) and *sc v f car* males in the order mentioned, produced 54.6 per cent. wild-type and 46.3 per cent. *sc v f car* female offspring; whereas when *sc v f car* males were used first, only 13 per cent. of the F_1 were *sc v f car* and 87 per cent. were wild-type. Since Lobashov's tables show only combined data, they do not indicate the behavior of individual females. Nevertheless, from the data of the present paper, it would appear that the results obtained by Lobashov are the kind to be expected if on the average fewer sperms were transferred by the *sc v f car* than by the Florida male, and if in addition, viability were poorer among embryos homozygous for *sc v f car* than among those heterozygous for these genes.

Selective fertilization, following either sperm mixture (Lobashov) or displacement (Dubinin), would require differences in vigor or mortality among sperm types which would depend on their genetic constitution. Dubinin has suggested that a biochemical antagonism may

exist between the sperm originally deposited and that subsequently received, so that the former is eliminated. This view has been criticized adversely by Lobashov; certainly our experiments show that all the types of sperm that we have tested can remain mixed, with two or three types functioning during several days of egg laying. Experiments by Muller and Settles were designed to determine whether differential mortality takes place while sperm is stored in the receptacles of the female of *Drosophila*. They found that aging the sperm did not appreciably affect the ratio of sperm of different types utilized in fertilization, even when the sperm had been stored in females kept as long as three months at 10 degrees C. It was also found that sperms carrying deficiencies and duplications function equally well in transferring these altered genoms to the egg. These and similar experiments led Muller and Settles to the conclusion that it was "highly unlikely that either natural or artificial agents do or can cause a selective elimination of spermatozoa, according to their hereditary composition, sex-determining types, 'strength,' or 'potencies.'"

In the course of this discussion we have outlined our reasons for believing that the results of our experiments permit similar conclusions.

SUMMARY

The number of sperms transferred by a 4- to 5-day-old wild-type male of *D. melanogaster* in a single copulation has been found by actual count to approach 4,000. In successive copulations the number rapidly decreases, until after a few matings no sperm is transferred. By the next day, however, additional sperm may be available for transfer. The amount of sperm transferred in a single copulation is only sufficient to guarantee fertilization of all eggs laid during the first few days by the average female. On subsequent days the percentage of sterile eggs increases, so that toward the end of the egg-laying period practically all eggs deposited are unfertilized.

A measure was made of the ability of sperms of three types of males, namely, wild-type, Curly/Glazed and plexus brown speck, when used in all possible mating sequences, to take precedence in fertilizing the eggs of plexus brown speck females. The Curly and Glazed offspring from these crosses were slightly more frequent than the wild-type; the plexus brown speck represented only about one sixth of the total progeny. Similar proportions were found among the offspring of plexus brown speck females, which were permitted to lay their eggs in the same bottle, after each had mated with only one of the types of males available. Such similarity suggests that the differences in frequency of different classes of offspring following polyandry are referable to differential viability of the different types of embryos and larvae, and not to differences in vigor or mortality of the various types of sperms leading to selective fertilization.

LITERATURE CITED

- Auerbach, C.
1941. *Jour. Genetics*, 41: 255-265.
- Demerec, M. and B. P. Kaufmann
1941. *AM. NAT.*, 75: 366-379.
- Dubirin, N. P.
1928. *Zh. Exp. Biol.*, 4: 131-159. In Russian.
- Duncan, F. N.
1930. *AM. NAT.*, 64: 545-551.
- Huettner, A. F.
1924. *Jour. Morph.*, 39: 249-265.
- Lobashov, M. E.
1939. *Compt. Rendus (Doklady) Acad. Sci. U.R.S.S.*, 23: 827-830.
- Muller, H. J.
1940. *Jour. Genetics*, 40: 1-66.
- Muller, H. J. and F. Settles
1927. *Zeit. ind. Abs. u. Vererbungsl.*, 43: 285-312.
- Nabours, R. K.
1927. *AM. NAT.*, 61: 531-538.
- Nachtsheim, H.
1927. *Verb. V. int. Kongr. Vererbungsw.*, 1143-1147. *Zeit. ind. Abs.*
..... *u. Vererbungsl. Suppl. II.* 1928.
- Nonidez, J. F.
1920. *Biol. Bull.*, 39: 207-230.
- Ward, L.
1923. *Genetics*, 8: 276-300.

THE DISCOVERY OF THE NEMERTEAN GORGONORHYNCHUS AND ITS BEAR- ING ON EVOLUTIONARY THEORY

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WHILE collecting on the shore between tide-marks, soon after my arrival in Bermuda in 1932, I found a small but by no means inconspicuous Nemertean under a stone in company with polychaets and molluscs. This was the second species of Nemertean I had seen in Bermuda. I could scarcely believe my eyes when, on touching this new worm, a series of thin white threads were shot out in place of the normal proboscis. I sectioned the worm and wrote a description of a new and unique species of *Cerebratulus*. Suspecting an error, I searched unavailingly all the literature I had, but came eventually upon a review (Coe, 1932) of W. J. Dakin's letter to *Nature* in November, 1931, entitled "A New and Peculiar Marine Nemertean from the Australian Coast." This review was written by W. R. Coe, the American authority on the Nemertea, who, when I met him in New Haven at the end of 1931, had kindly offered to give me the notes and sketches of the worms he had himself collected in Bermuda some years before.

Dakin described the proboscis of his new worm as follows:

The proboscis of the nemerteans usually consists of an introverted tube in a proboscis sheath, and it is everted like a finger of a glove that has been pulled "outside in." This new nemertean has also a proboscis which is retractile within a proboscis sheath, but the proboscis is branched. The branching is of the dichotomous type. During eversion, which takes place almost explosively, the short main trunk first appears, then this divides and the finer and finer branches appear, but since each one of these is the result of an evagination the effect is almost indescribable. It is as if a large number of lively, wriggling, minute worms had been shot out. The tip of the animal is like a gorgon's head.

From this noticeable feature Dakin coined the name *Gorgonorhynchus*, remarking on the affinities of the worm with the Lineidae and its close resemblance, except for

the proboscis, to worms of the genus *Cerebratulus*. He gave it the specific name "repens" in allusion to the explosive suddenness of the protrusion of the proboscis.

His worms were discovered in 1930 on the shore of Long Reef, New South Wales, by W. P. H. Dakin and M. G. C. Fordham. In 1931 specimens sent from the Madras Museum proved its existence in Indian waters. Later, specimens were found further north on the eastern coast of Australia and on the shores of two islands within the Great Barrier Reef, showing according to W. J. Dakin, who found them, that "the species occurred on the Australian coast in tropical waters and indicated how its occurrence might well extend in a continuous belt to the shores of India" (Dakin and Fordham, 1936).

No doubt could exist that I had found the same peculiar structural elaboration, unaware of Dakin's discovery, almost as far removed from the scene of that discovery as possible.

The Nemertean worms are a compact group of animals. Most of them are marine, free-living, elongated in form, ciliated, but unsegmented externally. Unlike the Turbellaria, with which they were once included, they possess an anus. The outstanding feature of the group, however, is the proboscis. Open any text-book of zoology, even the most recent, and you will find that the characteristic organ of the phylum Nemertea is this proboscis—a muscular introvert, capable of eversion and introversion through an anterior terminal pore, contained in its own closed tubular cavity and thus isolated morphologically from the alimentary canal and the rest of the body. It has been known and figured since the first published description of the "Long Sea Worm" by Borlase in 1758, but by most of the early writers it was regarded as the intestine, while the true alimentary canal was thought to be part of the genital system. It was not until 1847 that its nature as an independent organ was recognized by Frey and Leuckart. Nemerteans are found in the sea, in fresh water and on land. In "Das Tierreich" (1904) Bürger

described 309 species divided among 29 genera. New genera and species have since been discovered, especially from the deep sea, but in all Nemerteans hitherto described—pelagic, littoral, fresh water and land forms, even in the parasitic species—the proboscis conforms to the well-known pattern of a single eversible tube.

The genera *Cerebratulus* and *Lineus* are closely related and world-wide in distribution. Bürger (1904) divided the family Lineidae, the Heteronemerteans with lateral horizontal cephalic slits, into Lineinae, those without a caudal appendage, and Micrurinae, those which possessed one; but in preserved specimens the caudal appendage is nearly always missing and even in the living animal it is not always present, so that considerable difficulty has been experienced in placing species under the different genera. The discovery that neurochord cells were invariably present in the brain of the swimming forms suggested a new basis of differentiation, and it is now accepted that a worm of the Lineid type, capable of swimming and possessing neurochord cells in the brain, will normally carry a caudal appendage and should be placed under *Cerebratulus*, while worms that creep and coil, but do not swim, and that do not possess neurochord cells, belong to the genera *Lineus* or *Micrura*.

Gorgonorhynchus is typically Heteronemertean in structure. It swims like *Cerebratulus* and, like *Cerebratulus*, it possesses a caudal appendage and a pair of neurochord cells. It is, in fact, a *Cerebratulus*, with the exception of the dichotomously branched proboscis, and in this one feature it differs not only from its own near relatives but from all other Nemerteans. The Bermuda *Gorgonorhynchus* is smaller than the Australian species. The body varies in length up to 12.9 cm and is 2 mm wide when in motion, but may be 4 mm wide and much shorter when at rest. Small specimens may be white; larger ones are bright yellowish- or brownish-red down the back, the color fading at the sides which, with the underside, are uncolored. The bilobed pinkish blur marking the position of the brain is conspicuous. The posterior end of the

body is flattened and forms a swimming blade or oar and the caudal appendage is 1-2 mm long. I have separated it from the Australian species under the name *Gorgonorhynchus bermudensis*.

The discovery of a new Nemertean is not usually an event of great significance. New species and new genera are constantly being added to the list of known forms. But there are suggestive features about the occurrence of *Gorgonorhynchus* that lead to seductive fields of speculation, and it may be that here is indeed a new clue to an old mystery.

It is curious that in all the years of marine research and the gathering of specimens from different parts of the world such a striking deviation from the normal has remained unnoticed. It seems more than a coincidence that at two places as remote from one another as Australia and Bermuda discovery should take place independently and nearly simultaneously. Why has this worm with its extraordinary proboscis not been found before? There does not appear to be any circumstance in its life history or habits that would explain its long seclusion and sudden emergence. The comparatively recent discovery of *Pelagonemertes* by the *Challenger* expedition, of *Nectonemertes* by Verrill and of a host of pelagic forms since described by Coe, Brinkmann and others from the oceans of the world is simply the result of an investigation of an unexplored region by special methods. One expects to meet the new in the unknown. Taking an example from another group of animals—the prawn *Anchistioides antiquensis* was discovered in Bermuda in 1934 by F. A. Brown under a light that he was using at night to catch specimens of the prawn *Penaeopsis*. One or two specimens had previously been captured by J. H. Welsh using the same method but they were then not recognized as new. Continuation of the observations has resulted in the collection of more than 1,200 specimens, but there is no record of a capture in the daytime. For three years I have been trying to discover their hiding places by day

without success. The pelagic Nemerteans and the prawn *Anchistioides* would never have been discovered but for the special methods used. They were there all the time, presumably, the worms living perpetually in the deep waters of the open ocean, the prawns hidden in the daytime and coming to the surface at night round the Bermuda shores at certain periods of the moon. Nobody guessed their existence until the deep sea net or the light disclosed it. With *Gorgonorhynchus* the case is different. It is a littoral form; it has no strange habits; its capture does not involve anything but hands to turn over stones and eyes to see. It is not particularly small; and it is brightly colored. Yet the only answer biology can give when asked how such a departure from the normal had never been discovered is that it was there but it was overlooked. And the only alternative answer, impossible though it may sound, is that it was not there.

It can not be denied that the shores of Australia, of India and of the islands of the Great Barrier Reef may yet conceal strange new animals. It is perhaps reasonable to assume that *Gorgonorhynchus* escaped the notice of the collectors of the *Astrolabe* in 1826-29, although a number of species of Nemertea from New Guinea, New Zealand and New Holland (as Australia was called by the early navigators) were taken and described by that expedition. It is possible to suppose that for more than a hundred years it escaped discovery in Australian and Indian waters. Bermuda is a different story. The islands are only 19 square miles in area and the beaches have been the field of interest of many zoologists. The *Challenger* collected in Bermuda, and although no Nemertean was described from the shore, *Geonemertes agricola* was discovered; and McIntosh (Vol. 12) listed and described thirteen species of Polychaet taken between tide-marks (*i.e.*, under stones, since the shores are practically devoid of seaweed) two of which are commonly found in company with *Gorgonorhynchus*. Alexander Agassiz paid two visits to Bermuda, but there is no

record of any collection by him. A. E. Verrill, of Yale, with a party of four workers in April and May, 1898, and again in March, April and May, 1901, this time with A. H. Verrill and W. G. Van Name, lived in the islands and collected intensively all groups of invertebrates. Verrill (1900, 1901) wrote two reports covering the Nemerteans and he described several new species. In his first report (1900) referring to the Turbellaria and Nemertea, he says: "Particular efforts were made by our party to make good collections of these groups." He described two new species of Lineus (*L. albocinctus* and *L. albonasus*) and, from memoranda made by Coe, he reported *Taeniosoma curtum* (Hubrecht) Coe, calling it "the most interesting as well as the most common species" which "has been recorded from the Mediterranean, from Mauritius, Chili, Samoa, the Fiji islands and other localities in tropical and sub-tropical seas of both hemispheres." He noted a fourth Nemertean—"100-150 mm long and about 3 mm diameter in extension, found at low tide in tenacious tubes coated with shell-sand. Light yellow anteriorly, becoming pale ochre yellow posteriorly. Proboscis long and slender. It is probably a Lineus but has not been carefully studied."

I have already remarked that Gorgonorhynchus was the second species of Nemertean that I found in Bermuda. The first was *Baseodiscus delineatus* (Hubrecht), described by Verrill under *Taeniosoma curtum*. I agree with Verrill's estimate of its abundance. I have collected *L. albocinctus* and *L. albonasus*. I shall refer again to the fourth worm—the Lineid with the long and slender proboscis—but I should point out that tube-building is an unusual nemertean accomplishment, though it is known in species of Tubulanus, Valencinia and Cerebratulus. It is, of course, a common activity of Polychaets, one of which, *Terebella magnifica* (*Eupolymnia m.* of Verrill) builds, on the undersides of stones, tubes that are very tenacious and coated with shell-sand and it is always on such stones and often in company with *Terebella* that Gorgonorhynchus is found.

In his second report Verrill (1901) says: "Two or three additional species of Nemertean were obtained in 1901 but they have not yet been fully studied. The most interesting one was taken singly, two or three times under stones at low tide. It was 150-175 mm long and 4-5 mm broad. It was somewhat flattened, except anteriorly. Its color was bright orange scarlet. No eyes were seen. It appeared to be related to *Polia* or *Eupolia*." Considerable numbers of another Lineid (probably *L. ruber*, which I have taken) were found in a rather brackish pond near Bailey's Bay.

I find it hard to understand how Verrill and his party on two occasions overlooked what now appears to be the second commonest Nemertean in Bermuda. Verrill was more than an acute observer and naturalist with a wide knowledge of invertebrates generally. He had himself studied the Nemertea, and had identified, noted and sketched many of the several thousands of specimens collected during the explorations of the United States Fish Commission from 1871 to 1887. How came it that he missed *Gorgonorhynchus*?

Coe himself collected in Bermuda in June and July, 1903. I now have the notes and sketches of the 19 species that he found during that visit, but no worm with a branched proboscis is among them. He collected *Baseodiscus delineatus* (No. 3 of his list and "very common"), *Lineus albocinctus*, *L. ruber* or *socialis*, *Micrura purpurea* (Verrill's *L. albonasus*), and certain other worms possessing eye-spots, which he assigned to various genera (*Tetrastemma*, *Zygonemertes*, *Euborlasia*, *Drepanophorus*) and which could not possibly be mistaken for *Gorgonorhynchus*. Of the remainder no name was suggested for No. 1; No. 5 was "*Micrura*"; No. 6 was queried "*Cephalothrix*" as was No. 8. In each case the proboscis was specifically mentioned. Of No. 1 Coe says:

Usually bright red or orange red inclining to brownish red in intestinal region. Some individuals are bright scarlet and others orange red while immature specimens are often much paler sometimes being reddish flesh color. Some are bright orange throughout, others have a greyish tone over a deep

red ground color. When sexual products are mature the intestinal region inclines towards ochre or cream color. Fully ripe males are sometimes rosy flesh in the region distended by the sexual products. Caudal cirrus colorless. Proboscis usually pale flesh color.

I did not find this worm until June, 1940, when four were taken under one stone at Coney Island. One of them was closely enveloped in a mucous coat loaded with mud. Coe's No. 5 was small and white with a conspicuous bright reddish mark on the dorsal surface of the head near the tip. It has been taken recently in the Reach by Dr. Hope Hibbard. Nos. 6 and 8 may belong to the genus *Cephalothrix*, as Coe suggested. I have not found them. The proboscis was, however, "slender and colorless" in the former; "small, slender and short" in the latter.

From Verrill's description only one specimen of the yellow Lineid was taken and it can be inferred that the locality of its capture was Baileys Bay. Verrill's second unknown worm was slightly longer than this one and also broader for its length. He does not suggest that it was the same as that found on the previous excursion, but it was taken "singly, two or three times" under stones at low tide. Baileys Bay and Hungry Bay are mentioned as collecting localities in the section on the Nemertea in this report. His suggestion that it was related to *Polia* conveys the impression that lateral horizontal cephalic slits were not present, yet he did not remark upon a distinction between head and body that would normally be expected among the *Baseodiscidae*. Coe collected intensively and successfully during his two-months stay in Bermuda. He found the worms that Verrill had named in his first report, with the possible exception of the unknown Lineid and he discovered some worms of other genera that I have not yet found. His description of No. 1 covers the color variations of immature and mature specimens. It is evident that a number of individuals were examined and this, in addition to its position as No. 1 of his list, suggests that it was a common form. He does not remark on cephalic slits or eye-spots, but in his colored sketch neither can be seen. Except for the presence of

the caudal appendage it corresponds with Verrill's second unknown worm, the orange scarlet *Polia*, and having now seen specimens I have no doubt that it is in fact identical with it. The caudal appendage, however, decisively bars its inclusion with *Polia* (*Baseodiscus*); it proclaims instead its affinity with the tailed Lineids *Cerebratulus* or *Micrura* and thus suggests the possibility of identity with Verrill's yellow Lineid.

In 1903 the Bermuda Biological Station for Research was established, due to a large extent to local interest in marine life. Summer sessions were held at the Flatts until 1907, when permanent quarters were opened at Agar's Island near Hamilton. Still more workers visited the islands and collected on the beaches, but none of them discovered *Gorgonorhynchus*. I arrived in Bermuda on December 31, 1931, and found my first specimen on April, 1, 1932. It shot its proboscis completely. I noted that "When the animal was irritated a series of 10-12 thin white threads were extruded in place of the single normal proboscis of the phylum." In August, 1935, Dr. L. Hyman was collecting *Turbellaria* in Richardson's Cove. Unaware of the discovery of *Gorgonorhynchus* she brought two specimens of it to me. She had observed the protrusion of the proboscis and was puzzled by it, just as I had been, and just as the collectors of the type in Australia five years before would have taken little notice "had it not been for the beautiful and startling proboscis which was suddenly protruded when the worm was lying in the hand."

Verrill's first report deals with the *Turbellaria*, *Nemertea* and *Annelida*. His principal collecting grounds were Baileys Bay and Flatts Inlet. Castle Harbour is mentioned twice. His second report covers nearly every group of the littoral invertebrates. Castle Harbour is given as the collecting locality on 22 occasions, Long Bird Island and Hungry Bay are mentioned 16 times each, Harrington Sound 9 times and a number of other places, Coney Island, Tucker's Town, Baileys Bay, the

Reach, once or more. The majority of references to habitat are "under stones at low tide."

On the map of Bermuda (Fig. 1) I have marked the places where I have found *Gorgonorhynchus* and they have always been found under stones at low tide. Their abundance can be gauged from the fact that in twenty

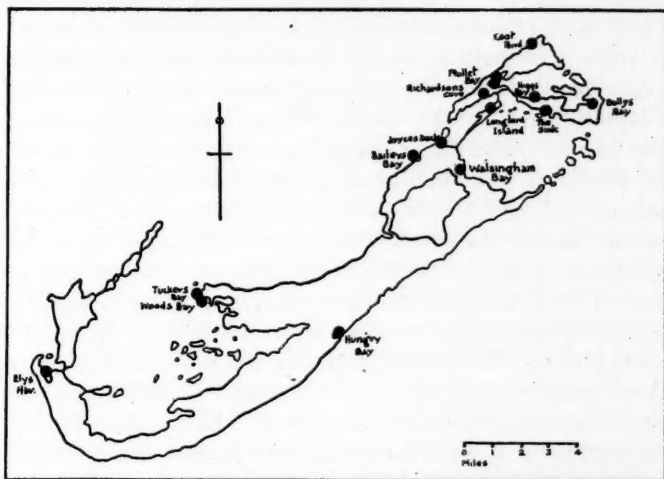


FIG. 1. Map of Bermuda showing places where *Gorgonorhynchus* has been found.

minutes at Baileys Bay in July, 1939, I secured two specimens; the first stone I examined at the head of the Sink, St. David's, was sheltering two specimens (May, 1940) and two days later at Walsingham, on the other side of Castle Harbour, the third stone examined yielded one specimen. Hungry Bay was a favorite collecting ground when the Biological Station was situated on Agar's Island. I visited the bay in March, 1940, and in an hour and a half at low tide I collected five specimens of *Baseodiscus delineatus* and three of *Gorgonorhynchus*. How is it that *Gorgonorhynchus*, which is now so common, was not seen by naturalists and experts at one or other of the places they visited? It may be objected that all the

worms captured had shot the proboscis completely as did my own first specimen. Nevertheless, I saw the act and, in ignorance equal to my own, Dr. Hyman discovered it also. I can say at once that partial protrusion would not give the impression of a normal proboscis. The single trunk is extremely short and eversion is, as Dakin says, almost explosive. No explanation based on the possibility of misconception of this kind can be accepted. Neither is there any ground for the suggestion that seasonal or other periods of rarity or disappearance may be the root of the matter. I have taken specimens in every month of the year. Up to 1939 *Gorgonorhynchus* was a novelty to be collected and displayed to interested visitors. For this reason my records over the eight years since its discovery are not as complete as they might be. From the evidence of last year (1940) there is reason to suppose that it could have been captured at any time during the whole period, certainly during the summer of any year. Dakin comments on its abundance and distribution in Australian waters, expressing surprise at the range and numbers of the specimens collected. At the place of discovery, Long Reef, Colloroy, New South Wales, where it occurs "in considerable numbers," it was obtained "at every season of the year during the past four years."

It is, of course, conceivable that *Gorgonorhynchus* could have been introduced recently into Bermuda either in the natural course of its own methods of distribution or by artificial and presumably accidental transport, and that, following introduction, it rapidly and successfully colonized the beaches. What data we have count against a natural introduction, for, though it may be asserted with some truth that the nemertean fauna of the world is relatively little known, such a conspicuous type would almost certainly have been observed. I can not believe that dispersal took place from Australia or India through the Mediterranean, or round the Cape of Good Hope, without leaving some trace. Both are well-investigated localities, the former from Naples and Marseilles, more recently

from Ghardaqua in the Red Sea, and the latter in the course of Stephenson's ecological surveys of the South African coast. It seems still less likely that dispersal was across the Pacific and round the Horn or via the Panama Canal and the West Indies. There could have been no gradual invasion of shore line such as is indicated by the occurrence of Mediterranean forms on the west coast of South Africa (Wheeler, 1934); and while transport by ocean currents, with or without that most useful of accessories, the floating log, has undoubtedly led to a considerable spread of the Nemerteans, I do not see that it can have been effective in this case. There remains the accidental introduction by man, for which there has been in recent years a much greater potentiality than formerly. Fishes and other marine animals (iguanas and penguins) have for some years past been transported alive from the Pacific islands for exhibition at the Bermuda Aquarium. There is no evidence that Gorgonorhynchus is found on any of the islands in question, but fortunately the first collection of these Pacific vertebrates was brought to Bermuda in April, 1933, *i.e.*, after the discovery of the worm. I think that the chance of accidental introduction previous to this is not worth consideration. By eliminating the possibility of recent introduction we face a clear-cut alternative: either Gorgonorhynchus was present all the time but remained undiscovered by Verrill, Coe and others, or it has arisen somehow *de novo*, sometime between 1903 and 1932. It should be observed that *this is the only case that has ever been presented of the discovery of a new type in a small and uniquely isolated locality that had been examined many times previously not only by trained observers but by specialists in the group of animals to which the type belongs.*

Dakin gives the traditional explanation in suggesting that "the occurrence of Gorgonorhynchus at Bermuda seems to indicate that its distribution may be world-wide—at least on the shores of tropical and warmer temperate seas." Underlying it is the idea of the evolution of

the branched proboscis in the far-off ages of geological time; and it could be, of course, that *Gorgonorhynchus* once spread over temperate and tropical seas from which it has now largely disappeared. This is the classical Darwinian explanation. When we examine the world incidence and distribution of the branched proboscis we face the same alternative as when the inquiry is confined to the occurrence of *Gorgonorhynchus* in Bermuda. I can not too strongly emphasize the fact that this is not merely the discovery of a new genus among a somewhat obscure group of animals. This branched proboscis is something new to science. *Gorgonorhynchus* is a *Cerebratulus* in body, but its proboscis lies outside the long-accepted definition of the phylum and class Nemertea. It is an innovation in nemertean architecture. It illustrates the transformation of an existing simple organ into one more complex. Either it was present, but remained undiscovered through years of marine research, or it has arisen recently, suddenly and for all practical purposes simultaneously at places so remote from one another that its appearance is inexplicable by any accepted theory of the method and process of organic evolution. Admittedly the former is the simpler alternative. It throws the origin of the modification back into the past. The explanation of the sudden appearance and erratic distribution becomes a commonplace of accidental oversight, coincidence and juggling with continental masses. Had the branched proboscis long been known elsewhere in the world, its appearance in Bermuda would not have excited comment. The case for accidental oversight would have been overwhelming, for anything suddenly emerging lies under suspicion of being previously concealed. The fact that a new organ, obviously derived from a simpler form of the same organ, has made a wide-spread appearance in the world, when there is evidence, at least in one place, that it was not there until quite recently, suggests that the second alternative should receive serious consideration.

How could the branched proboscis arise? We must suppose that it was preceded by and developed from the simple normal form, and there is no inherent difficulty in picturing the bifurcations, in planes at right angles to one another, that result in the ultimate 64 twigs of the fully-formed proboscis of *Gorgonorhynchus*. The normal nemertean proboscis possesses a retractor muscle from its tip to the wall of the proboscis sheath or rhynchocoel. Eversion of the proboscis is caused by the pressure of contraction of the muscular wall of the rhynchocoel, transmitted by the fluid which fills the closed cavity. Relaxation of the muscles of the rhynchocoel combined with increased tension in the muscles of the proboscis itself cause a reversal of the process, which may be helped by the retractor muscle. *Gorgonorhynchus* has no retractor muscles. It has no difficulty in invaginating the proboscis, however, and so avoids the problem of the disposal of the 64 muscle strands that would otherwise be necessary. There can be no doubt that the retractor muscle is only accessory to the function of withdrawal since it is lacking in two species otherwise quite normal. It is perhaps significant that these two species (*Zygeupolia litoralis* and *Cerebratulus lacteus*) are both Lineids. Whether the proboscis is branched or single, its eversion or retraction is under the control of the muscles of the rhynchocoel wall and the proboscis itself, yet *Gorgonorhynchus* possesses flap valves in the axils of the proboscis branches. These unique structures have been described in detail by Dakin and Fordham, who suggest that because of them "all branches of the same denomination need not be everted or retracted simultaneously." Their presence also suggests that *Gorgonorhynchus* could maintain pressure in its everted proboscis when normally nervous fatigue of the control by rhynchocoelomic and proboscis muscles would bring about retraction. By this means a crown of sensitive tentacles could be spread for considerable periods ready for the capture or entanglement of food. This hint at the sedentary life of a sea anemone

or tubicolous polychaet worm suggests a connection between tube-forming habits and branching of the proboscis.

Among the species of Nemertean known to form tubes are *Cerebratulus lacteus* (on the authority of Verrill) and the unknown Lineid of Verrill's first Bermuda report, which may be, as I have shown, the "Polia" of his second report, identical with Coe's No. 1 worm, and so with the specimens I have found, one of which was enveloped in a mucous coat. Others are *Tubulanus* (*Carinella*) *annulata* and *T. linearis* (McIntosh, 1873) *T. nothus* (Wheeler, 1934) and *Tetrastemma validum* (Wheeler, 1934). Dakin points out that the only reference in the literature of the Nemertea to branching of the proboscis is McIntosh's description of an incomplete specimen of a *Carinella* from the Shetland Islands (McIntosh, 1873). McIntosh's figure shows an enigmatic portion of body with an undoubted proboscis protruding from a broken surface. It had apparently been torn out of the rhynchocoel but it displays a bifurcated tip, each free end bearing part, at least, of a retractor muscle of its own. Is this a foreshadowing of the branched proboscis of *Gorgonorhynchus* and can it be correlated with the tube-building habits exhibited by both *Tubulanids* and *Lineids*? Is there a tendency in these Nemerteans to the sedentary life, kept in check among the *Tubulanids* by the retention of the retractor muscle and allowed full play in the group which has, in three species, dispensed with it? I must admit that the proboscis of *Gorgonorhynchus* is not experimentally capable of prolonged eversion and that the ability of the worm to swim suggests an active predatory life rather than an evolution along sedentary lines, but neither point carries weight if *Gorgonorhynchus* has recently appeared in the world. It is not yet adjusted to its environment. It seems to me as fair to anticipate the future as it is to imagine the past. There is, moreover, a better chance of ultimate proof.

Consideration of the development of a multiple proboscis from a single one leads to a critical examination of the theories of organic evolution. All around us, in the different kinds of animals and plants that inhabit the earth, we see the outcome of past events. Every living species gives the impression of having been planned some time ago, yet the palaeontologists point to their fossils and we see that changes have occurred—extinctions and emergences—some apparently gradual, some sudden and nearly all on a vast scale. We sort our animals and plants into genera, into families, orders, classes and phyla by the recognition of similarities or common characters. Because of these common characters we infer relationship, the derivation of different kinds of animals and plants from common ancestors, more or less remote in time depending on the closeness or otherwise of their similarities, but we have no absolute proof of this relationship or of the evolution which is implied. The evidence that we see, the generations of plants, of dogs, horses, pigs and other animals, all giving rise again and again to offspring like themselves, suggests indeed a majestic continuity arising somehow in the remote past, and, for all we can observe to the contrary, reaching out unchanged into the infinite future. Certainly closer scrutiny reveals dissimilarities in successive generations, slight differences in shape, color and disposition, and these variations have been utilized by man through his recorded history in shaping, to some extent, his domestic stock to his use or fancy. From the observed fact of variation Darwin and Wallace postulated the theory of natural selection and showed how, given sufficient time, the differentiation of species might have occurred. By a continuance of the process, "new species would multiply in many directions, until at length from one or more originally simple forms the earth would be peopled by the infinite varieties of plant and animal organisms which have in past ages inhabited or do at present inhabit our globe" (Turner, 1900).

If the reader accepts the implications of the second alternative as to the origin of the branched proboscis it will be obvious to him that natural selection can not have been operative. Time is the essential component of natural selection and its strength is that it proceeds with infinite slowness by imperceptible stages and is thus proof against experiment. There remains mutation in the sense of de Vries and Bateson, experimentally demonstrated by Morgan in *Drosophila*, with the wider application hinted at by many writers and supported by Willis's work on the distribution of endemic plants.

Willis (1940) follows the differentiation theory of Guppy that "In the far back days of damper and more uniform climate most of what are now the large families were formed each at one stroke by well-marked mutations, and they then slowly began to grow in size by further mutations." The mutations followed one another with increasing rapidity, but by less and less strongly marked stages, so that evolution has proceeded in the reverse direction from that postulated by Darwin. Natural selection can eliminate but it has no power to create. "If the newly formed plant could pass through the sieve of natural selection, and escape the dangers that threatened its very existence when it first began, it might then begin to spread, and once established in several places it would be, comparatively speaking, safe."

The theory of origin by mutation was based on the propagation of a single mutant. Darwin himself did not condemn the mutant theory of the origin of new species, but he rejected the idea of Mivart that several wonderfully changed individuals appeared simultaneously within the same district (Darwin, *a*). This idea has nevertheless been expressed by many writers and there is some evidence in its favor. Thus Weissmann (1909) states that "in the case of the green caterpillars with bright longitudinal stripes numerous individuals exhibiting this useful variation must have been produced to start with." J. S. Huxley (1925) reported that *Gentiana campestris* in

quite separate localities in Savoie threw off a variant with a white corolla and pale green leaves, growing in situations similar to the areas where the type plant was abundant, and suggested that "the probable explanation of such groups is that they are all descended from a few or probably a single mutant ancestor" but a later report (Druce, 1926) of the same variant occurring in Zetland and the island of Balta suggests that the same mutation had occurred in other places. Discussing the discovery of *Typhlops braminus* in Mexico, Gadow (1913) was led to the assumption "that among the countless generations of Typhlops in Mexico some have hit off exactly the same kind of permutation and combination of those characters which we have hitherto considered specific of *braminus*. . . ."

The suggestion of orderliness inherent in the conception of identical mutants thrown off at the same time regardless of locality or environment opens the way on the one hand for vitalistic theories and the postulation of a direction to evolution as in the "Orthogenesis" of Eimer and in Bergson's vital impetus, and on the other hand to the "Hologenesis" of Rosa. Rosa suggested that in every living thing there is a load of potentialities which are gradually used up by successive generations. Each species is thus "wound-up" at its inception and when its potentialities are unfolded it reaches maturity and at this point a change takes place in the germ plasm resulting in the sudden appearance of two daughter species which differ from each other and also from the mother species. By this theory new species will appear simultaneously over a wide area. Although the observed facts can be explained in this way, the theory suffers from the common disability of theories of evolution that although it might have happened in the past it does not seem to be happening now.

When the significance of the sudden appearance of the Gorgonorhynchus-type was realized, it appeared to me that only a form of mutation would explain the phe-

nomenon. It appeared further that the mutation must be multiple or even universal and that at least two species of Lineid were involved since two species of Gorgonorrhynchus have been found. This one case, a peculiarity in an obscure group of animals, may be considered poor material to compare with the sudden wide-spread appearances of the great groups of animals and plants in past ages; but there is another case—the loss of scent in the musk plant at the beginning of this century—which is closely parallel, though in the reverse direction. “The total disappearance within recent years of the scent of musk, *Mimulus moschatus* Dougl., is one of the most puzzling of plant phenomena. A native of North America, it was introduced into Great Britain from British Columbia in 1826 by the botanist David Douglas. It quickly became a garden favorite and the yellow rather insignificant flowers are still a familiar sight in cottage windows. The plant has become naturalized in certain parts of the British Isles and New Zealand, where it was taken by the early settlers. At the beginning of the present century the sweet-smelling musk was hawked from door to door in London suburbs. It appears that the loss of fragrance was first noticed in Britain in 1909. Vilmorin (*‘Les plantes de pleine Terre,’* 5th Ed., 1909) describes it, suggesting that the loss had not been noticed in France and there is conclusive evidence that in some localities the failure to produce the characteristic perfume was not generally apparent until after 1916. Sir Arthur Hill, director of Kew, in the presidential address, British Association, Section K (Botany) in 1930 said that as a result of exhaustive inquiries in Great Britain and western North America it had been established that plants of musk with the old-fashioned and distinctive fragrance were no longer to be found even in their native habitat. Correspondence with New Zealand shows that the same thing has happened in all stations where the plant was previously known to have been scented” (*Nature*, 134: 54, 1934).

Had *Mimulus* lost its scent in Great Britain and New Zealand only, some explanation on the ground of change in the environmental conditions might have been attempted, although the suddenness of the loss such a long time after introduction at two places so far distant from one another would have imposed severe conditions on any such theory. But that a distinctive character, in fact from the point of view of man, esthetically and financially, *the* distinctive character, should disappear from the plants in their native surroundings as well as from those at the other side of the world practically simultaneously defies orthodox reasoning. To outward appearance *Mimulus* is still *Mimulus*. Had it not been for the trade based on the distinctive character, would the loss of that character have been noticed? Or even if noticed here and there, would the defection have been followed up before it was too late to trace the suddenness and simultaneousness of its occurrence? "There is reason to believe that the extinction of a whole group of species is generally a slower process than their production . . .," Darwin stated; but "In some cases, however, the extermination of whole groups, as of *Ammonites*, towards the close of the secondary period, has been wonderfully sudden. . . ." In disappearances as in appearances there is precedent among the great groups for abruptness.

If *Gorgonorhynchus* has arisen by mutation in recent years its forerunner, a *Lineid* with a normal proboscis, should be included among the observations of the earlier workers. Stimpson and Schmarda described *Nemerteans* from Australia, New Zealand and Ceylon years ago, but the only recent records are those already quoted of Verrill and Coe in Bermuda. I have drawn attention to the species alluded to as "*Polia* or *Eupolia*" and No. 1 of Coe's list, found by both of them, and only recently by me. This worm is a *Lineid* with a caudal appendage and long cephalic slits, but it has neither the shape nor the color of *Gorgonorhynchus* and it does not swim. These characters, owing to the possibility of linkage, do not

preclude the idea of mutation. There is indeed the chance by isolation and development of the eggs to establish a direct mutation relationship. I should record the fact that my specimens of "Polia or Eupolia" seemed curiously inert. The one in the mucous tube broke across again and again without a sign of life like a flattened pencil of soft stone, but whether this un-nemertean sluggishness indicates the decrepitude of old age remains to be seen. I can only point out that a common species of Lineid has apparently become rare in Bermuda while a new type of Lineid is now common.

The universal occurrence of chromosomes in plant and animal cells and their behavior in the pairing processes of ovum and sperm supports the idea that some kind of unit is involved in the perpetuation of characters from one generation to the next. The concept of the gene originated in the minute study of the chromosomes, and, although not directly descended from the earlier theories of Darwin and Weismann, is their modern equivalent. According to J. B. S. Haldane (1932),

Genes, the genitalia corpora of Lucretius, reproduce themselves at each cell division and are handed down from parent to offspring. The genes in an organism determine how it will develop and behave in a given environment. The process of reproduction of a gene is not perfect. Occasionally a gene produces another gene of a different type. This process is called mutation and has never been shown to be adaptive still less to perpetuate an acquired habit. Evolution is due to the fact that only a few of the possible combinations of genes survive.

The genes themselves are usually pictured as definite units containing one or more molecules reproducing themselves either chemically by duplication or organically by fission. Thus Morgan (1916) says: "I do not know of any *a priori* reason why a factor may not fluctuate, unless it is, as I like to think, a chemical molecule." And M. F. Guyer in his address in 1929 to the American Association emphasizes the biological aspect by pointing out that genes must be nourished like other living things since they multiply and grow and apparently display the other characteristics of living matter. The linkage of char-

acters is dealt with by the association of genes—"genes exist in definite proportions and are arranged in a definite order. The whole gene-complex is divided up among separate chromosomes which in *Drosophila* have been shown to correspond to the linkage-groups established by genetic experiments" (Huxley, 1926). A further conception of great significance due to Morgan is the deduction backed by experimental evidence from *Drosophila* that species are to be thought of as groups of genes and that, as related species have a good many genes in common, similar mutations are likely to occur in different but related species.

The theoretical machinery for the sudden appearance of new species and new forms of a higher grade thus appears to be an established trend in modern thought, but the release mechanism, the initiator of change, is considered either as a fortuitous gene disaster or the effect of environment. It is an observed fact that individuals of the same species with a common origin and a similarity of genetic constitution tend to grow at the same rate and to age and die at the same time. The assumption that genes are living units, variable by accretion during growth to which they are subject, presupposes for them also a course of life and a time of dissolution or death. The immortality of the gene may be as illusory as the immutability of the elements. Are not radium, actinium, polonium, uranium and thorium usually described as changing spontaneously from one elemental form to another, changing moreover in their own time and suffering no interference from man to affect the process either in rate or result? Mutational changes can be produced by heat or x-rays, *i.e.*, by change in the environment, but it is beyond belief that an environmental change took place simultaneously in British Columbia, Great Britain, France and New Zealand to cause the loss of scent in *Mimulus*. Only an internal inevitable disruption of some sort can explain it. The death of a gene simultaneously within the species would not necessarily result in the

death of the species. It might bring change, a re-shuffling and perhaps a rebirth, outwardly signalized by a new species, a new genus or, at very rare intervals, a new class or phylum. It might on the other hand bring the loss of a character; it might mean complete and sudden extinction. Dispersal brings changes of environment. A modification occurring in one environment might be fatal when it occurred to individuals in another. Again, changes in the environment can affect the growth of the gene so that in one place their life is increased, in another shortened, for the environment immediately takes the new arrival in hand to shape by selection, to grant pre-ferment or to eliminate.

I have ventured to put forward my view because it carries my conception of the gene to a natural conclusion and because it appears to offer an explanation of what is to me otherwise an incredible coincidence. I need hardly point out that the sudden appearance of a new type in almost any other place and circumstance would not have produced the same effect. I do not think that there is any place in the world with the same degree of isolation as Bermuda, whose area is so small and whose fauna has been so closely under observation during recent years.

Apart from the theoretical machinery of the process is the possibility of proof of its result. If one or more species of *Cerebratulus* have suffered a mutation in recent years, it appears quite likely that the same mutation will occur in allied species. New species of *Gorgonorhynchus* should be discovered where there may or may not be previous data of the Nemertean fauna. Direct observation on "*Polia* or *Eupolia*" in Bermuda should decide whether this species is moribund; also whether it is the mutation mother-species of *Gorgonorhynchus* by development from the eggs. The problem of the Nemertean proboscis, the constant intimate connection of the proboscis system with the nervous system, the advantage of the branched form over the normal, all need elucidation.

The anatomy of this group has appeared so uniformly invariable in the past that, except for species determination by taxonomists and the regeneration experiments of Coe, its peculiarities have been largely neglected. It is just that uniformity which makes the appearance of a new type conspicuous. It adds one more riddle and perhaps a clue to the problem of evolution.

LITERATURE CITED

- Coe, W. R.
1932. *Biol. Abstr.*, 6, 8-9, August-September.
- Dakin, W. J., and M. G. C. Fordham
1936. *Proc. Zool. Soc. London*, Pt. 2, pp. 461-483.
- Darwin, C.
a. "Origin of Species," 6th Ed., London, p. 202.
b. *Ibid.*, p. 294.
- Druce, G. C.
1926. *Nature*, 117: p. 270.
- Gadow, H.
1913. *Nature*, 92: 145.
- Haldane, J. B. S.
1932. *Nature*, 129: 857.
- Huxley, J. S.
1925. *Nature*, 116: 497.
1926. *Nature*, 118: 903.
- McIntosh, W. C.
1873. *Monogr. British Annelids*, Ray Soc., London.
- Morgan, T. H.
1916. "A Critique of the Theory of Evolution."
- Turner, W.
1900. Inaugural Address, British Association.
- Verrill, A. E.
1900. *Trans. Conn. Acad. Sci.*, X, Pt. 2, pp. 595-670.
1901. *Trans. Conn. Acad. Sci.*, XI, December, pp 15-62.
- Weissmann, A.
1909. *Darwin and Modern Science*. Cambridge, 1909, p. 28.
- Wheeler, J. F. G.
1934. *Discovery Repts.*, IX, pp. 215-294.
- Willis, J. C.
1940. *The Course of Evolution*. Cambridge.

THE PHENOMENON OF HOMOEOSIS

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HOMOEOSIS, sometimes called heteromorphosis, is the alteration of one organ of a segmental series from its own characteristic form to that of some homologous member of the series (Bateson, 1894). The phenomenon has long been known from occasional instances of abnormal regeneration occurring naturally in some arthropods and it has been produced experimentally in others. More important from an evolutionary standpoint are hereditary homoeotic changes which are known to occur in many insect orders.

Experimental homoeotic regeneration was first described by Herbst (1896) in the decapod *Palaemon*, in which an antennalike structure developed in place of an extirpated eye-stalk. Krizinecky (1914) destroyed the optic ganglion in the larva of the mealworm *Tenebrio molitor* and observed the regeneration of antennalike organs in place of the eye. The regeneration of tarsus-like structures in the place of extirpated antennae was found by Przibram (1909) in the praying mantis, *Sphodromantis bioculata*, and in certain beetles (1919a) and by Cuenot (1921), Brecher (1924) and Borchardt (1927) in the walking stick, *Dixippus morosus*. Przibram (1919b) used a hot needle to burn the antennae of mature larvae of the saw-fly, *Cimbex axillaris*. When the antennae regenerated, their terminal segment bore one or two claws, pulvilli and hairs characteristic of a tarsus.

Homoeotic changes occurring in nature, which may or may not have been hereditary, have also been reported. Wheeler (1896) found an antennalike structure growing out of the coxa of the right prothoracic leg of the midge *Dilophus tibialis*. Bethe (1896) described a crab, *Carcinus maenas*, in which one of the abdominal swimmerets was replaced by a large thoracic walking leg. Giesbrecht

(1910) found a stomatopod, *Squilla pallida*, with an antenna growing in the place of an eye after he had produced this type of regeneration experimentally by extirpating the eye. In his monograph on regeneration, Korschelt (1927) quotes several reports of various crustacea found in which the mandible was replaced by a claw-tipped thoracic leg or swimmeret, or in which the thoracic legs were replaced by swimmerets.

Many arthropod groups exhibit hereditary homoeosis in nature. Lebedinsky (1925) mentions the Lepidopteran family Zygaenidae in which the metathoracic wings are completely similar to the mesothoracic wings. Wasmann (1900) discovered the very aberrant Dipteran, *Termi-toxenia*, in which the wings are much reduced and intermediate in character between wings and halteres. Bezzi (1916) described a number of Hymenoptera, Neuroptera, Strepsiptera and Coccids in which the metathoracic wings are reduced to appendages resembling halteres, whereas in some parasitic Hymenoptera, Orthoptera and Homoptera, the mesothoracic wings may be halterelike.

Several homoeotic mutations have occurred in *Drosophila*. The first two to be described were bithorax and bithoraxoid (Bridges and Morgan, 1923). Bithorax is characterized by a more or less complete change of the normal metathorax into a segment resembling the normal mesothorax. The extent of the change is variable; it is often unequal on the two sides, and sometimes overlaps the wild or normal type. A structure bearing bristles and resembling the mesonotum and scutellum covers the sides and more or less of the dorsal surface of the metathorax. The halteres or balancers are modified in various ways: some are swollen and hairy, others are inflated and sack-like, suggesting the type of wing found in the mutant "inflated," and still others are flattened and winglike, bearing veins. The metathoracic legs of some flies bear an apical tibial bristle, normally absent on the metathoracic leg but present on the mesothoracic leg. Bi-

thoraxoid (not an allele of bithorax) resembles bithorax having inflated halteres and a less well-defined hairy structure on the dorsal surface of the metathorax. Several alleles of bithorax have been found which differ from it in their penetrance, expressivity and viability. Bithorax-2, bithorax-3 and bithorax-w are more extreme than the original bithorax, whereas bithorax-34e and bithorax-D, a dominant allele, are less extreme. A third homoeotic mutant, tetraptera, similar in many details to bithorax, was described by Astauroff (1927, 1929). Tetraptera was much more variable phenotypically than was bithorax; most of the flies in the tetraptera stock were completely normal. The phenotypes of tetraptera include a series of changes from a normal haltere to a completely developed metathoracic wing, with all intermediates.

A different type of homoeotic mutant, aristapedia, was described by Balkashina (1929). In this mutant the arista (the plumose tip of the antenna) is replaced by a tarsuslike organ consisting of several, up to five, segments. Again there are large variations in the phenotype, forming a series from a reduction of the antenna to two segments, in which the arista and the third segment of the antenna are completely missing, through many intermediates to a structure of seven or eight segments, consisting of the three antennal segments and a four- or five-segmented structure identical with a tarsus bearing a pair of claws, pulvilli and a saw-toothed bristle. A less extreme allele, aristapedia-Bridges, and a more extreme allele, aristapedia-Spencer, have been found. A similar mutant was described by Sturtevant (1929) in *Drosophila simulans*.

In a third type of homoeotic mutant, proboscipedia, described by Bridges and Dobzhansky (1933), the oral lobes which normally form the proboscis are totally lacking and in their place is a pair of tapering, jointed appendages, extending laterally and tipped with strong, claw-like bristles or with a heavy branched bristle resembling an arista. The structure which replaces the oral lobes

may therefore resemble either a tarsus of an antenna. The phenotype is again very variable, the appendages differing considerably in length, size, distinctness of segmentation and in the terminal bristles. The rest of the mouthparts are also modified: the pseudotracheae disappear completely, the labrum and maxilla change shape, and the maxillary palpus fuses with the maxilla, so that the mouthparts of a proboscipedia fly resemble somewhat the biting mouthparts of lower insects.

A fourth type of mutant is one in which there is an antennalike structure instead of an eye or in combination with a rudimentary eye. All intermediates between a small hairy knob and a segmented, palpuslike structure of three or four segments are found. This may not be a true homoeotic phenomenon, however, but merely the result of a splitting of the antennal disc early in development. One part of the split disc may form the normal antenna, and the other part the abnormal one which grows in the eye region and partially or completely suppresses the development of the eye. No detailed study of this mutant has been made as yet, but it has been reported as a high allele of the mutant kidney (Goldschmidt, 1929, 1940; Gottschewski and Ma, 1937; Valadares, 1938) and as a high allele of Lobe (Goldschmidt, 1940).

In the fifth type of homoeotic mutant, *tetraltera* (Goldschmidt, 1940; Villee, 1942), the normal mesothoracic wing is replaced by a halterelike appendage, with a large intermediate series between this and the normal wing. The extreme expression of the mutant produces a fly with four halteres. In addition, the mesonotum and scutellum may be reduced or missing, changing the appearance of the dorsal mesothorax to that of a metathorax.

These mutants have several features in common which set them off more or less from other mutants:

1. The phenotypes are very variable, forming a series from a normal, unchanged organ to a complete, homoeotic replacement of it by a homologous organ.
2. There are large variations in penetrance, *i.e.*, vari-

ations in the percentage of flies homozygous for the mutant which show the character phenotypically.

3. The degree of symmetry in the expression of the character varies greatly; animals with complete symmetry are rare.

4. There is a low degree of right-left correlation in the expression of the character (Astauroff, 1930).

Goldschmidt (1940) pointed out the general feature that the homoeotic organ is primarily a palpus, a primitive appendage containing a few segments which may specialize into an antenna, a haltere or a tarsus.

The group of homoeotic mutants found in *Drosophila melanogaster* are interesting genetically because, with the exception of the homoeotic Lobe allele mentioned by Goldschmidt (1940), all are located in the same region of the right arm of the third chromosome (proboscipedia, 47.7; tetraltera, 48.5; tetraptera, 51.3; aristapedia, 58.5; bithorax, 58.8; bithoraxoid, 58.8 +, kidney, 64.0). This fact was mentioned by Balkashina (1929) as a coincidence when she found that aristapedia was located in the same region as bithorax, bithoraxoid and tetraptera. Goldschmidt (1938) mentioned this fact as supporting his hypothesis that there are no "genes" but that the chromosomes themselves act as units in heredity in controlling the normal development of the animal. On this basis there is no accidental clustering of homoeotic genes in this region; rather, this whole region of the right arm of the third chromosome acts in normal development in regulating the determination and development of the imaginal discs. Various upsets in the pattern of this part of the chromosome, *i.e.*, the homoeotic mutants, produce the different homoeotic phenotypes. No additional evidence has been found to support or disprove this explanation. No visible aberrations in the structure of the salivary gland chromosomes of these mutants have been observed.

A knowledge of the embryology of the homoeotic mutants is essential to an understanding of their action. A developmental study has been made in only two mutants,

in aristapedia by Balkashina (1929) and in tetraltera by Villee (1942). Balkashina found that the segmentation of the antennal disc begins in the normal fly in the 4- or 4½-day larva, just before pupation, whereas in an aristapedia fly it begins in the 2-day larva, soon after the leg discs begin to segment. By the time the larva is 4 or 4½ days old, its antennal disc has divided into five segments. In the 3-hour pupal stage, the normal antenna reaches its definitive three-segmented condition, whereas the aristapedia antenna consists of seven or eight segments at this time. The further development of the normal antenna consists of an extension of the third segment and a differentiation of this into the arista. In the aristapedia appendage, further development and differentiation are typically leg-like: the segments become cylindrical and are covered with a thick coating of chitin, the bristles and hairs develop in a tarsuslike pattern, and claws and pulvilli form on the end of the last segment. Balkashina concluded that the effect of the aristapedia gene in development is to stimulate the imaginal disc of the antenna to segment at an earlier stage, and to guide the differentiation of the disc towards that of a tarsus.

A general explanation of the action of homeotic loci in producing their effects was derived by Goldschmidt (1938) from the facts of the development of aristapedia described by Balkashina, as follows: All the imaginal discs have identical potencies very early in development. Each becomes mature, *i.e.*, able to be determined, at a certain stage in the development of the animal different from the others. A series of evocators, one for each type of disc, is given off by the germ, each at the proper time to affect the proper disc which has just become mature. Sometime during or before the second day of larval life an evocator is given off by the germ which diffuses into the six leg discs and causes a rhythmic subdivision of the distal end of the anlage, producing the typical tarsus segmentation. Normally only leg discs are in a proper condition to react to this induction, but any disc in the proper

stage of development will react to this induction by tarsus formation. The action of the aristapedia gene, therefore, is to speed up the early differentiation of the antennal disc, causing it to become mature at the same time as the leg discs. It is the tarsus evocator and not the aristapedia gene itself which causes the formation of the tarsus on the antenna. Such a system would explain the appearance in proboscipedia flies of both tarsuslike and aristalike structures, depending upon whether the imaginal discs producing the mouthparts (the labial buds) have had their time of determination shifted to coincide with that of the leg or of the antenna. The fact that phenocopies of certain of these mutants have been produced (Enzmann and Haskins, 1939; Rapoport, 1939) shows that these same times of determination may be shifted by external agencies as well as by inherited mutations.

Braun (1939, 1940) and Waddington (1939) demonstrated that the developmental system of the aristapedia antenna is identical with that of the legs and not that of the antenna. The antennal tarsi of aristapedia flies were shown to be affected by the leg mutants *dachs*, approximated and four-jointed, but not by the antennal mutants *thread* and *aristalless*. Waddington pointed out that in aristapedia-Bridges and compounds of aristapedia-Bridges with aristapedia, a series of forms is obtained in which different proportions of the arista are affected. These aristae are not intermediates between legs and normal aristae; certain parts are strictly leglike, whereas others are strictly aristalike, the transition zone being very narrow. The transition occurs from proximal to distal, the distal tip becoming leglike only if all the rest of the arista has been changed. According to Goldschmidt's time relation theory, this indicates that the maturation of the antennal disc and the diffusion of the leg evocator into the disc are not completely synchronized; only the proximal part of the antennal disc is mature and can be affected by the leg evocator; the rest of

the disc becomes mature later and undergoes induction by the normal arista evocator and forms a normal arista.

In each of the homoeotic mutants which have been investigated it has been found that the homoeotic locus may do more than simply change one appendage into another; it may affect the development of the whole disc from which the appendage springs. In addition to changing the oral lobes into a labiumlike organ resembling a pair of antennalike or tarsuslike appendages, the labrum, maxillae, maxillary palpi and other mouthparts of proboscipedia flies may be changed to resemble the biting mouthparts found in lower insects, indicating that the entire labial disc has been affected. In bithorax and tetraptera, in addition to the change of the haltere to a wing, the metathorax may be enlarged and bear bristles resembling those of the mesothorax. In tetraltera, in addition to the change of the wing to a haltere, the mesothorax may be reduced and the scutellum and bristles removed so that it resembles a metathorax. A slight extension of Goldschmidt's theory of the development of homoeotic organs would account for the multiple changes observed in these mutants. In tetraltera, for example, if the wing has developed as a haltere while the rest of the thorax has developed normally, we can conclude that only the wing bud part of the dorsal mesothoracic disc was affected by the above system and determined to develop into a haltere instead of a wing. If, however, the tetraltera locus acts earlier in development or perhaps at a greater rate, the whole dorsal mesothoracic disc may be influenced abnormally by the evocator of the metathorax and determined to develop into a metathorax. The stages in the reduction of the mesothorax and the elimination of its parts, described in my recent paper (1942), may be regarded as steps in the change of the mesothorax into a metathorax. In each step a greater portion of the mesothoracic disc was affected by the evocator of the metathorax and determined to develop as a metathorax, just as more

of the arista became tarsuslike in the successive stages of the aristapedia series described by Waddington and again due to slight differences in the stage of development of the dorsal mesothoracic disc when induction occurred. A similar explanation would hold for the variations in the metathorax observed in tetraptera and bithorax, and for those in the mouthparts other than the oral lobes observed in proboscipedia.

The studies of homoeotic phenomena have revealed many facts important in embryology and comparative anatomy. The mutants bithorax, tetraptera and tetraltera clearly demonstrate the homology of wing and haltere and mesonotum and metanotum. The mutant aristapedia and the regeneration experiments on other forms indicate the homology of the antenna and tarsus; the insect antenna is a homologue of the mouthpart-leg series of segmental organs, and not a separate pre-oral structure as has been suggested by some comparative anatomists. The mutant proboscipedia shows that the oral lobes of Diptera are homologous to the labium of other insects, and are not the derivatives of maxillae, as was supposed by Lowne (1890). The basal part of the proboscipedia organ may represent a modification of the glossae and paraglossae of lower insects, whereas the lateral parts compare with the labial palpi of lower insects, no trace of which is normally present in the oral lobes of flies. The presence of tarsuslike and antennalike structures on these modified oral lobes demonstrates the homology of these mouthparts with the antenna-mouthpart-walking leg series of appendages of other arthropods.

The various phenotypes produced by the mutant tetraltera indicate the relative order of determination of the parts of the dorsal mesothoracic discs (Villee, 1942). It may be concluded that the wing is the last part of the disc to be determined, since reductions in it may occur without simultaneous reductions in the thorax, whereas changes in the thorax are always accompanied by large changes in the wing. The scutellum is the last part of the thorax to

be determined, since the scutellum may be absent without any other change in the thorax and its bristle pattern; but in all flies in which the imaginal hypodermis has failed to fuse in the dorsal midline, resulting in various abnormalities in the mesonotum, the scutellum is missing. The formation of the normal bristle pattern is probably dependent upon the meeting of the imaginal hypodermis in the dorsal midline, for when this fails to occur the bristle pattern is very abnormal and many of the bristles are missing.

The effect of temperature on the penetrance of homoeotic mutants was first reported by Astauroff (1930), who found that the penetrance of tetraptera varies directly with the temperature, from about 1 per cent. at 17° C. to about 35 per cent. at 25° C. In tetraltera, on the other hand, I found (1942) the opposite relationship, namely, the penetrance varies inversely with the temperature, from less than 1 per cent. at 29° C. to over 35 per cent. at 14.4° C. These contrasting relationships between temperature and penetrance are interesting in view of the opposite embryological processes involved: in the tetraptera phenotype, the change of a haltere anlage to produce a wing, in the tetraltera phenotype, a change of a wing anlage to produce a haltere. The action of temperature on development in general is that of a differential acceleration or retardation of certain processes in relation to others. It may therefore be assumed that the production of a wing instead of a haltere requires the differential acceleration of some reaction or reactions which is increased by higher temperature during or before the determination and differentiation of the wing and haltere discs; whereas the production of a haltere instead of a wing requires the differential retardation of these same or similar processes which is increased by lower temperature.

Goldschmidt (1940) emphasized the importance of the facts obtained from the studies of these homoeotic mutants in a general analysis of evolution in terms of his

concept of systemic mutations and macroevolution. He pointed out the taxonomic parallel to the tetraltera mutant in the aberrant termitophile Dipteran *Termitoxenia*. In comparing the various phenotypes produced by the tetraltera mutant with the *Termitoxenia* types given in Kemner's (1940) review of the group, I found that one of the phenotypes intermediate between a wing and a haltere which resembled neither very closely was almost identical with the *Termitoxenia* wing. The mutant tetraltera thus produces an animal whose wings resemble those of *Termitoxenia*, a member of a completely different family of Dipterans. The mutant proboscipedia produces mouthparts resembling those of lower orders of insects; no other Dipteran has mouthparts resembling even remotely those of proboscipedia flies. The presence of one instead of two pairs of wings is one of the characters distinguishing Diptera from other insect orders, yet the mutants bithorax and tetraptera produce animals with two pairs of wings.

The importance for evolutionary considerations of these mutants which produce changes in the phenotype characteristic of different families or orders is evident. They serve as models of the method of macroevolution. To produce the oral lobe type of mouthparts from the biting mouthparts of lower insects in evolution, for example, it is not necessary to postulate the gradual accumulation of many micromutations for the oral lobe type; rather a single mutation affecting early embryological processes suffices to explain the production in a single step of this new type. Animals having the intermediate types of mouthparts necessary on the Neo-Darwinian hypothesis would be unable to feed. Mutations controlling the speed of differentiation, the gradients of segmentation, the nature of the evocator or the time of induction of the different discs could produce at one step changes in the phenotype of the segmental organ of macroevolutionary importance.

LITERATURE CITED

- Astauroff, B. L.
1927. *Z. eksper. Biol.* (Russ.), Ser. A., 3: 1-61.
1929. *Arch. f. Entw-mech.*, 115: 424-447.
1930. *Zeit. f. ind. Abst. u. Vererb.*, 55: 183-262.
- Balkashina, E. I.
1929. *Arch. f. Entw-mech.*, 115: 448-463.
- Bateson, W.
1894. "Materials for the Study of Variation." London.
- Bethe, A.
1896. *Arch. f. Entw-mech.*, 3: 301-316.
- Bezzi, M.
1916. *Natura* (Pavia), 7.
- Borchardt, E.
1927. *Arch. f. Entw-mech.*, 110: 366-394.
- Braun, W.
1939. *Nature*, 144: 114-115.
1940. *Genetics*, 25: 143-149.
- Brecher, L.
1924. *Arch. mik. Anat. u. Entw-mech.*, 102: 549-572.
- Bridges, C. B. and Th. Dobzhansky
1933. *Arch. f. Entw-mech.*, 127: 575-590.
- Bridges, C. B. and T. H. Morgan
1923. *Pub. Carnegie Inst. Wash.* 327.
- Cuenot, L.
1921. *Compt. Rend. Acad. Sci.*, 172: 949-952.
- Enzmann, E. V. and C. P. Haskins
1939. *AM. NAT.*, 73: 470-472.
- Giesbrecht, W.
1910. "Fauna und Flora des Golfs von Neapel." 33.
- Goldschmidt, R.
1929. *Biol. Zentr.*, 49: 437-448.
1938. *Physiological Genetics*. New York, McGraw-Hill.
1940. "The Material Basis of Evolution." New Haven, Yale University Press.
- Gottschewski, G. and S. Y. Ma
1937. *Zeit. f. ind. Abst. u. Vererb.*, 73: 584-597.
- Herbst, C.
1896. *Arch. f. Entw-mech.*, 2: 544-558.
- Kemner, N. A.
1940. "VI Congreso Internacional de Entomologia." Madrid. 275-294.
- Korschelt, E.
1927. "Regeneration und Transplantation." Berlin. 2 vols.
- Krizevsky, J.
1914. *Arch. f. Entw-mech.*, 37: 629-634.
- Lebedinsky, N.
1925. *Abh. theor. Biol.*, 22: 1-36.

Lowne, B. F.

1890. "The Anatomy, Physiology, Morphology and Development of the Blowfly, *Calliphora erythrocephala*." London, R. H. Porter.

Przibram, H.

1909. Experimental-Zoologie. 2. Regeneration. Leipzig und Wien.
1919a. *Arch. f. Entw-mech.*, 45: 52-68.
1919b. *Arch. f. Entw-mech.*, 45: 69-82.

Rapoport, J. A.

1939. *Bull. Biol. et Med. exp. de l'U. R. S. S.*, 7: 415-417.

Sturtevant, A. H.

1929. *Pub. Carnegie Inst. Wash.*, 399: 1-62.

Valadares, M.

1938. *Revista agronomica*, 25: 363-383.

Villee, C. A.

1942. *Univ. Calif. Publ. Zool.*, 49: 125-184.

Waddington, C. H.

1939. *Growth supplement*, 1: 37-44.

Wasmann, E.

1900. *Zeit. f. wiss. Zool.*, 67: 599-617.

Wheeler, W. M.

1896. *Arch. f. Entw-mech.*, 3: 261-268.

REVIEWS AND COMMENTS

EDITED BY CARL L. HUBBS

In this section reviews and notices are given of current publications on general biology and of specialized works which have an important bearing in this general field. Emphasis is given to books and major articles which fall within the special scope of *THE AMERICAN NATURALIST*, in that they deal with the factors of organic evolution.

REVIEWS AND COMMENTS are meant to include also such general discussions, reports, news items and announcements as may be of wide interest to students of evolution. Except as otherwise indicated, all items are prepared by the Section Editor, Dr. Carl L. Hubbs, University of Michigan, Ann Arbor, Michigan. All opinions are those of the reviewer.

Temperature and Evolution. Isolating Mechanisms. Genetic Control of Embryonic Development. Edited by TH. DOBZHANSKY. Biological Symposia, Vol. VI. Lancaster, Pa.: The Jaques Cattell Press, 1942: i-xii, 1-355, 73 figs., 2 pls. \$3.50.

THE BIOLOGICAL SYMPOSIA are becoming a potent force in the integration of biology. The seven volumes which have now appeared correlate a wealth of data and interpretation along many lines of general biology. As Dobzhansky writes in the Foreword to Volume VI, "genetics, embryology, systematics, physiology, ecology and cytology have in this volume, ceased to be distinct from each other." Happily biology is crystallizing from a mixture of sciences into one science, with different facets of interest. The evolutionary aspect is considerably stressed in the sixth volume, here under special review. This is as it should be, for evolution remains a central problem in biology.

Previous volumes include discussions on evolution. The "Symposium on Speciation," in Volume II, focused the views of a number of specialists on an important phase of evolutionary research, but was not reviewed in these columns because this symposium was first published in *THE AMERICAN NATURALIST*. Volume IV presented four very interesting symposia, respectively on "Population Problems in Protozoa," "Theoretical and Practical Aspects of Polyploidy in Crop Plants," "Experimental

Control of Development and Differentiation" and "The Species Problem." These also appeared in THE AMERICAN NATURALIST.

All three of the symposia comprising Volume VI (not elsewhere published) are of particular significance from the standpoint of evolution. They deal with "Temperature and Evolution," with "Isolating Mechanisms" and with "The Genetic Control of Embryonic Development." Together they present a considerable sector of current evolutionary thought. DOBZHANSKY's Foreword to the volume and PLOUGH's Introduction to the Symposium on Temperature and Evolution furnish a good start toward a modern philosophy of genetics and evolution.

Temperature as a factor in speciation is the central theme of the "Symposium on Temperature and Evolution." H. H. PLOUGH indicates that higher temperatures increase the rate of gene mutation. GERHARD FANKHAUSER states that extreme temperatures induce polyploidy in animals as well as plants and that polyploid races exist among parthenogenetic animals; but he is in doubt as to whether polyploid animals would succeed in nature and reserves judgment on the evolutionary significance of polyploidy in animals. Treating the relation of temperature to differentiation in *Drosophila*, GEORGE P. CHILD tells of phenotypic effects that simulate known genotypes, and justifies his statement that "these studies may lead to a better understanding of the effects of temperature in the differentiation of characters, the differences between wild and mutant types and the evolution of the wild type."

EMIL WITSCHI discusses "Temperature Factors in the Development and the Evolution of Sex," chiefly on the basis of his earlier studies on the evolution of local sex races in European frogs. A very interesting and significant adaptive correlation between the sex chromosome mechanism and the environmental temperature is detailed, but the conclusion that the fundamental differences must have evolved during the 20,000 years since the last

glaciation seems unwarranted: the different types may have arisen at a much more ancient time, and have migrated northward in early Postglacial time at about the same rate, so as to preserve a geographic pattern and environmental correlation that was established thousands of years earlier.

The contribution of *Drosophila* genetics to our knowledge of "Isolating Mechanisms, Evolution and Temperature" is presented by H. S. MULLER, in a thorough, informative and stimulating though at times perhaps overly theoretical and somewhat complicated discussion. WALTER LANDAUER deals with the interaction of hereditary potentialities and environmental temperature, particularly as indicated in his studies of a sport, the frizzle fowl. ALFRED C. KINSEY thinks that an evolutionary momentum (orthogenesis) may be involved in the development of north-south gradients in time and temperature of emergence of gall wasps. In treating the relation of temperature to the development of frogs and other animals, JOHN A. MOORE emphasizes the modifications which adapt these animals to life at different temperatures.

The "Symposium on Isolating Mechanisms" stresses the paramount significance of isolation in the origin of species, and emphasizes throughout the wide variety of isolating mechanisms that are effective, even in small groups of plants and animals. The contributors and the groups they treat are: G. LEDYARD STEBBINS, JR., plants; ALBERT P. BLAIR, toads; ALFRED C. KINSEY, gall wasps; J. T. PATTERSON, *Drosophila*. The publication of sample data from Dr. Kinsey's race analyses in the Cynipidae is a highlight in this series of four excellent papers, which together constitute a major contribution to our knowledge of speciation.

The third symposium, "On Genetic Control of Embryonic Development," strikes deeply into an emergent subject of profound importance. VICTOR CHANDLER TWITTY, VIKTOR HAMBURGER and SEWALL WRIGHT, all master biologists, are the contributors.

Visual Mechanisms. Edited by HEINRICH KLÜVER. Biological Symposia, Vol. VII. Lancaster, Pa.: The Jaques Cattell Press, 1942: i-viii, 1-322, 84 figs., pl. 1. \$3.25.

EXPANDING one of the symposia held in connection with the Fiftieth Anniversary of the University of Chicago this volume focuses the views of twelve prominent investigators on the problem of how animals see. Dr. Klüver remarks that specialization among the students of vision is so great that the various investigators in this field are finding it difficult to understand one another. How much more difficult it is, for biologists of unrelated disciplines to follow the progress of research on visual mechanisms. Herein lies a main reason for the publication of symposia such as this one.

The first contribution, by SELIG HECHT, treats "Energy Relations in Vision." Most of the other contributions deal primarily with the physical and chemical aspects of vision, in man and the mammals used by the experimental biologists. The anatomical, physiological and psychological aspects of vision are all treated. The advances that are recorded in the knowledge of the sense of sight are grand and bewildering to the uninitiated.

A few of the contributions present the knowledge of vision from the zoological and evolutionary viewpoints, and will be of prime interest to the readers of *THE AMERICAN NATURALIST*. In treating the intricate relation between "Visual Systems and the Vitamins A" GEORGE WALD reviews his noteworthy discovery that freshwater fishes irrespective of relationship contain a retinal pigment (porphyropsin) different from that found in marine fishes and most other vertebrates (rhodopsin), and that most euryhaline fishes possess both types of pigment.

The phylogeny of the visual cells is treated by GORDON L. WALLS, the leading student of comparative ophthalmology. He tells a scientific story of great interest—of the origin and differentiation of the visual cells, and of their modifications to meet the peculiar needs that are entailed by the different habits and the diverse habitats character-

istic of various animals. This chapter will induce many readers to consult Dr. Walls' large book on "The Vertebrate Eye and Its Adaptive Radiation," being published by the Cranbrook Institute of Science.

Genetics for Medical Students. By E. B. FORD. London: Methuen & Co., 1942: 1-162, figs. 1-10. 7s. 6d. net.

In this Age of Text Books one is apt to overlook another college text. Here, however, we find one that commands our attention. A primary reason is that human genetics is still an emergent branch of science, in its pure form as well as in the applied aspect of medical genetics. Despite an importance and a need that are clearly obvious, genetics is just breaking its way into the medical curriculum. The very few texts on genetics for medical students, such as Frazer Roberts' in England and Snyder's in the United States, have appeared only during the last few years. The field has not begun to be crowded, but even if it were a text so fresh and so scholarly in its approach as Ford's would be a welcome addition. The modern viewpoints on genetics, and on cytology as briefly expressed in an appendix, render the book of value not only to the beginning medical student but also as a refresher to practitioners. It would be good medicine too for both students and workers in the various lines of social science, and for the public in general. Ways in which genetic data may be useful to the physician are emphasized, along with indications of how doctors trained in genetics can help accumulate data on human heredity.

The blood groups and the taste test are given particular attention, and treated as examples of polymorphism—one of the author's special interests. In an inclusive point of view polymorphism is described as "the occurrence together in the same habitat of two or more forms of a species in such proportions that the rarest of them cannot be maintained by recurrent mutation." Little indication is given to the circumstance that simple mendelian ratios

are generally characteristic of polymorphism, whereas inheritance that is now best interpreted as multifactorial is typical of geographical variation (and of systematic distinctions in general); the author makes the contrast on ecological grounds. As though with a pardon, examples of unifactorial inheritance are treated as atypical because the heterozygotes are to some degree intermediate. May not this condition be more common than is generally indicated?

Fishes of Western South America. I. The Intercordilleran and Amazonian Lowlands of Peru. II. The Pampas of Peru, Bolivia, and Northern Chile. With a Revision of the Peruvian Gymnotidae, and of the Genus *Orestias*. By CARL H. EIGENMANN AND WILLIAM RAY ALLEN. Lexington: University of Kentucky, 1942: i-xv, 1-494, pls. 1-22, figs. 1-48, 1 map. \$5.00.

THIS magnificent quarto volume, published, under a trust fund, in celebration of the 75th anniversary of the University of Kentucky, is a very welcome though belated report on explorations conducted by the authors from 1918 to 1920. It is chiefly a contribution to systematic and faunal ichthyology, but contains sections of interest to others. There is good reading and much geographical, ethnological and historical data in the chapters dealing with the authors' field work, with other ichthyological explorations in the same general region, with the fisheries and native methods of fishing, and with South American native fish lore. There is also an important and thorough analysis of the distribution of the fishes, which is of particular interest in connection with fauna of the high Andean lakes. Interspersed in the long Annotated List of species are reviews of the literature and lore of the *candirú*, the supposedly urinophilous fish, and of the "man-eating" *piranhas*; an account of *Arapaima*, one of the giants among fresh-water fishes; a revision of the Peruvian Gymnotidae; a thorough study of the cyprinodont genus *Orestias*, which is confined to the Andean pampas at elevations of 12,000 to 16,000 feet and has

undergone striking radiative speciation, particularly in Lake Titicaca; and a brief chapter on mimicry, inserted after the discussion of the systematic status of the fish which the authors treated in 1921 as a dead-leaf mimic.

NOTICES OF NEW BOOKS

Insects of Guam—I. By O. H. SWEZEY and many other authors. Bernice P. Bishop Mus. Bull. 172, 1942: 1-218, 10 pls., 10 figs. (distributed by Department of Entomology, Experiment Station, Hawaiian Sugar Planter's Association, Honolulu).—The first of two sets of reports by systematic entomologists on the insect fauna of Guam, this volume contains much basic information on the problem of the origin and speciation of island faunas. Nearly all of the text, however, is detailed taxonomy. The few passages of general systematics were prepared by O. H. Swezey and by Elwood C. Zimmerman, who is known to AMERICAN NATURALIST readers for his analyses of the speciation of insects on the Pacific islands.

General Entomology. By S. W. FROST. New York: McGraw-Hill Book Co., 1942: i-x, 1-524, frontisp., figs. 1-406. \$4.00.—Insects seem to have been designed to illustrate biological principles. For this reason entomology is particularly adaptable to topic treatment—provided the writer is a master of the enormous literature of entomology, and a real biologist. Professor Frost demonstrates himself to be both. He writes of insects as living creatures, forming part—a major part it is true—of the living world. Morphology and classification are not neglected, but rather coordinated into the general biology of the Hexapoda. The emphasis is more intensely ecologic than evolutionary. Speciation and genetic phenomena, though so well illustrated by insects, are hardly mentioned. Evolutionary biologists, however, will share with college students the good fortune of having available such a wealth of significant biological information.

Applied Entomology. New 4th Edition. By H. T. FERNALD AND HAROLD H. SHEPARD. New York: McGraw-Hill Book Co., 1942: i-ix, 1-400, figs. 1-373. \$3.50.—Fernald and Shepard have modernized this well-known introductory text on general and economic entomology. New methods for the control of pests have been included, if these are regarded as being more practicable and efficacious than the methods previously in use. Most of the material is presented in taxonomic order: less than one-tenth of the book is devoted to a general discussion of insects and to their anatomy and development, and even less space is accorded the general chapters on economic entomology.

Life Histories of North American Flycatchers, Larks, Swallows, and Their Allies—Order Passeriformes. By ARTHUR

CLEVELAND BENT. Bull. U. S. Nat. Mus., 179, 1942: 1-538, pls. 1-70. \$1.00 (paper).—Like the previous volume, of this well known compendium, this book presents in detail much basic data on the biology of birds.

A Text-Book of Zoology. By T. JEFFERY PARKER AND WILLIAM A. HASWELL. Sixth Edition, Vol. II, Revised by C. Forster-Cooper. London (and New York): Macmillan & Co., 1940: i-xxiii, 1-758, figs. 1-656. \$9.00.—Neither time nor space has been found for the inclusion of an adequate review of the new, extensively revised edition of the master text-book of zoology in the English language. We therefore now give only this brief notice, with the advice that every vertebrate zoologist and every zoological laboratory should keep this volume close at hand.

Natural History and the American Mind. By WILLIAM MARTIN SMALLWOOD, in Collaboration with MABEL SARAH COON SMALLWOOD. New York: Columbia University Press, 1941: i-xiii, 1-445, 10 pls. \$4.25.—Thoroughly documented and written with enthusiasm, this book gives an interesting and clear picture of early natural history in America.

Trees of the Eastern United States and Canada—Their Woodcraft and Wildlife Uses. By WILLIAM M. HARLOW. New York and London: Whittlesey House (McGraw-Hill Book Co.), 1942: i-xiii, 1-288, 5 col. pls., "pls." 1-8, figs. 1-152. \$2.75.—This manual is well designed to facilitate the identification of the trees of the area and to give an understanding of their uses.

A Revision of Melanconis, Pseudovalsa, Prosthecium, and Titania. By LEWIS E. WEHMEYER. Ann Arbor: University of Michigan Press (Univ. Mich. St., Sci. Ser., 14), 1941: i-viii, 1-161, pls. 1-11. \$2.50.—A detailed systematic study of several genera of Fungi, with descriptions of new subgenera, sections, and species.

SHORTER ARTICLES AND DISCUSSION

FURTHER PROGRESS WITH ARTIFICIAL SELECTION

THE AMERICAN NATURALIST for September-October, 1937, contained an article entitled "Can Artificial Selection Produce Unlimited Change?" (Goodale, 1937). This article described the results of an experiment in selective breeding beginning with a single male mouse with a few—not more than thirteen—white hairs on its forehead, which at the time that article was written, had resulted in a stock of mice, each of which had a white spot covering much of its forehead above the eyes. The selective breeding was carried out within a strain closed to inheritance from sources other than this one male and the four self-colored females with which the strain began.

As the amount of white increased beyond the point where the individual hairs could be counted readily, a system of numerical grades was established, new grades being introduced as necessary. Grade 8, for example, represented by the mouse head shown at D, in Fig. 3 of the NATURALIST article, designates a spot covering most of the face above the eyes as far as the ears. In the highest grade at that time—grade 14, shown at E in the same figure—the white area above the eyes is like grade 8, but the white area also extends downward to the tip of the nose on one side of the face. Since then the amount of white has increased to an amount called grade 20. In this grade the white area begins on the top of the head, extends downward over the face in front of the ears but back of the eyes, across the rear of the cheeks and across the lower jaw. The front view of the head of these mice, except the ears, is entirely white.

As the amount of white on the head increased, white began to appear on the tail, feet and the central region of the belly. The belly spot did not appear until the head spot was larger than grade 8; and though it has never been seen in the control or unselected mice derived exclusively from the same five foundation mice as the selected strain, it separated from the head spot in some descendants of certain individuals of the latter strain which were mated with long inbred self-colored agoutis in order to investigate the nature of the changes which must have occurred in the chromosomes of this strain. Although several successive

generations of these segregates have been mated, using only mice with a belly spot as parents, about half the offspring have no belly spot. The others have a white belly spot varying in size from near zero to a third of the ventral surface. Other than this, no attempt has been made to study the inheritance of belly spot.

In the early stages of the work the white area on the head enlarged by gradual expansion, but by the time grade 8 was reached white areas—as mentioned above—had begun to appear in other regions of the body in the same general fashion that water pressing against a dike may break through in unexpected places. With the advent of grade 8 mice, white bands extending across each eye downwards towards the lower jaw appeared in many individuals. Perhaps if more attention had been paid to the appearance of white areas in other parts of the body, progress in increasing the total amount of white would have been more rapid. However, since cut-and-dry efforts at this stage of the investigation led to the conclusion that it would be advisable to work in some one direction, further efforts to produce white-faced mice were concentrated on widening a very narrow median line which extended from the tip of the nose upwards to the grade 8 spot in some mice. These efforts finally yielded grade 15 mice in which the whole face is white as far as the anterior margin of the eye, grade 16 mice in which the outer edge of the white area passes through the middle of the eye, grade 17 mice in which it clears the posterior margin of the eye, and, more recently, mice of grade 20, grades 18 and 19 being intermediate between grades 17 and 20.

Recent increases in amount of white on the head of the mice is accompanied in some instances by white areas of various sizes on various parts of the upper surface of the body between the fore and hind legs. However, mice with body white do not necessarily have the largest amount of white on the head, since it has appeared in mice as low as grade 14.

The amount of white on the body varies from a very small, scarcely visible spot to a band on one side covering one third the distance between the fore and hind legs and extending from the ventral surface to the mid-dorsal line. In some instances, the upper end of the band may be connected to the head white by a stripe along the mid-dorsal line as well as to a belly spot.

As it happened, the first mouse with white on the upper surface of its body was marked in the extensive fashion. In the next

litter from the same parents, another individual appeared similarly marked, except that the white band was on the right side instead of the left. The father of these mice had 70 children by a first set of five mates, of which only the two were above grade 17. Ten months after the first mating a daughter and four granddaughters were mated to him. They yielded 85 additional children of which 6 had markings, mostly small, on various parts of the upper surface of the body. The distribution of white on the heads of 7 mice was asymmetrical, the white extending considerably farther back on one side of the head than on the other. This male, then, bred much as other males of his time, save for the few exceptional individuals.

The first two exceptional mice—both males—were mated, one to two sisters one of which had two sons and a daughter, none of them exceptional. The other sister had no children.

The other son had 74 children, 25 from a half-sister. One son by this sister was similar to his sire; one was grade 18; and one daughter, grade 17. Of the remainder of this son's children, one daughter was marked like her sire and one was grade 17. The remaining children were unexceptional.

In the next generation the story is much the same, though it includes one mouse of grade 15 with a white shoulder patch, and others of grades above 13 with more or less white along the spine near the shoulder, or in the region of the vertical white band back of the shoulder. Altogether, these advances in amount of white on the head and on the body constitute a series graded in amount by small degrees but uncertain as to location.

Breeding several generations of the mice originating in mating cage 372, the one in which the first exceptional mice appeared, demonstrates once more the difference between phenotype and genotype, for these advanced phenotypes breed as all phenotypes of a continuously varying character breed, that is, back toward the existing average of the race. The average amount of white among their children has increased a little and the center of distribution of grades has advanced a little in the direction of selection, but the range of variation has not diminished. Moreover, due to variation in size and location on the body of the additional areas of white, the white markings on no two mice are exactly alike. Although in some individuals a sharp advance in total amount of white has occurred, the change in genotype seems to be merely a small advance in the direction of selection.

Six months after the appearance of the first mouse with much white, mice with white patches on the body began appearing among mice not descended from mating cage 372, associated, in the first litters, with grades 15 and 16 instead of grade 20, which did not appear until the second litters, thus confirming the deductions of the preceding paragraph.¹

In a sense every increase in the amount of white may be regarded as a novelty, but they differ in one very important respect from novelties which appear without design of the breeder, of which short ear, dwarf, hairless, rodless retina, shaker 1 and shaker 2 and many others listed in *Mouse Genetic News* for November, 1941, may be cited as examples. Though the breeder may perpetuate these novelties by suitable methods of breeding, he does not originate them. By contrast the advances in the direction of selection which appear in the course of selective breeding for some predetermined objective are produced at the will of the breeder, at least in the sense that a mechanic produces a hole by brace and bit at will. The chipping away of the material may be rapid or slow, depending on the nature of the material and to some extent on the character of his equipment. But the result—the hole—is the result of the intent of the mechanic, and not a spontaneous appearance. In this sense the increase in the amount of some or all of the white on these mice is the result of the intent of the breeder and not the mere perpetuation of a condition entirely outside his intent or expectation.

Spontaneous novelties—mutations—result from a change in one or more chromosomes. And since the chromosomes constitute the physical basis of inheritance, changes of some sort must arise in the chromosomes under selective breeding, even if they are nothing more than a reshuffling of existing genes. Though these changes may be identical with those that give rise to the spontaneous haphazard changes called "mutations," it is conceivable that they may be of a different character whose nature can only

¹ Previously an occasional spotted mouse which usually died before weaning had appeared at widely separated intervals. Very little attention was paid to these mice, they were so infrequent, so different from the others and lived so short a time that they could not be bred. In a branch line, originating in the same five foundation mice and under the same selective breeding program, certain spotted individuals with misshapen heads have appeared, some of which survived and were mated. These were mostly sterile and have never given rise to a spotted strain. Their relation to the spotted mice now appearing is uncertain.

be determined by future investigations. It is as desirable, then, to withhold judgment on their nature for the present, as it would be premature to include all advances in the direction of selection under the term "mutation" or to consider them due to reshuffling of genes.

Our knowledge of methods of selective breeding is not only very scant, but the methods available are not capable of accomplishing all that we might wish. We have not been able to direct the increase in white to the exact locations we would prefer it to appear. Nevertheless, when a boat or ship acquires a rudder and sails, it is no longer completely at the mercy of the wind and waves but comes sufficiently under the control of the navigator to reach a destination, even though it does not follow the exact course charted by the navigator. Thus the advances which have been made in the direction of selection by the progeny-test methods of breeding used in this work indicate that selective breeding is acquiring the genetic equivalent of rudder and sails.

Four stocks of mice, each one descended exclusively from the five foundation mice of the first paragraph of this article, are maintained in the mouse house at Mount Hope Farm. One stock, characterized by a few white hairs and propagated by random matings, is a continuation of the unselected or control stock described in the *NATURALIST* article. From this stock a new stock has been developed in which the few white hairs have been eliminated by progeny-test breeding. The other two stocks have been bred for more white. The rate of reproduction in one stock is superior to that of the other, and may account for greater progress in increasing the amount of white. However, it has not always maintained the lead.

These four stocks are in no sense species or sub-species. Nevertheless, if they had been found in a wild state, geographically or physiologically isolated from each other, their status as species or sub-species might at least be open to debate by systemetists.

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LITERATURE CITED

Goodale, H. D.

1937. *AM. NAT.* LXXI; September-October.

BLOOD GROUPS OF EURASIANS AND PARSEES IN
CALCUTTA

ENDOGAMOUS racial groups who live among racially distinct peoples, such as the Gypsies of Hungary, provide the best demonstration of the value of blood group distribution data for tracing racial affinities; only a few of such groups exist. Likewise the effect of racial intermixture is usually obscured because the half-breeds become absorbed in one of the ancestral races. Only in India is endogamy widely practiced among all the racial groups of a large area. Even there the blood group proportions in most of the original stocks involved are unknown and endogamy has not been strictly adhered to throughout history.

The Eurasians, or Anglo-Indians as they are now called, are socially segregated from both Indians and Europeans in India and are almost entirely an endogamous hybrid group.

The Parsees are a community with Near Eastern racial affinities who emigrated from Persia and have practiced endogamy in India for centuries.

It was therefore believed that the blood group distributions in these two communities would prove interesting.

EURASIANS (ANGLO-INDIANS)—HISTORY OF THE COMMUNITY

The Eurasians of India are found chiefly in the cities and are not necessarily of English descent, although they officially adopted the communal title of "Anglo-Indians" for political reasons after the first World War. Under the Hindu caste system the offspring of Hindu women and foreign men are seldom taken into their mother's caste, except in the matriarchal regions of Malabar and Assam.

From the early days of European settlements in India the great majority of the half-castes have been educated in western customs and have formed a separate Christian community.

The earliest European settlers in India were the Portuguese at the end of the fifteenth century; they were followed by the Dutch, French and British. From the beginning the Portuguese frequently married native women who had been converted to Christianity. It was always the policy of the Dutch that their soldiers, sailors and traders should marry natives; the offspring of such unions were, and are, given full European status in the East. I am indebted to Major H. Hobbs of Calcutta for drawing my

attention to an order of the British East India Company dated 1692 (Love, 1913) which read:

Encourage by all means that you can invent that our Souldiers do marry with the Native women, because it is impossible to get ordinary young women, as we have before directed, to pay their own passages, although Gentlewomen sufficient do offer themselves.

Major Hobbs further informed me, in a private communication:

Unfortunately the Order did not stand for long, as later it was ordered that none of these people were eligible for Government posts. There were many reasons for this, perhaps the most prominent being that men married Roman Catholics, against whom there was bitter animosity. These Catholics were descended from Portuguese and Indian women and were half-castes before the British settled in any numbers. The Portuguese were not satisfied with low-caste women; they took girls from higher caste families which led to their downfall by arousing the resentment of the people of the country. Among the untouchables and depressed classes the women are not ashamed of being attached to the household of a man who can look after them and treat them and their children well.

Muslim women were not available as wives or concubines for Europeans, so that the original Indian female ancestors of the Eurasians probably came chiefly from the Sudra and depressed communities of non-caste Hindus.

When communications between Europe and India improved fewer pure-bred Europeans retired in India, most of them returned to the West, while those of mixed ancestry remained in India where their children married into other Eurasian families. For the past century or more the British in India have attempted to maintain the purity of their racial strain. This ideal found expression in (1) the social segregation of the mixed community, who until recently were officially called Eurasians, (dusky families of the old Portuguese and Dutch mixed strains were also put into this group socially and politically) and (2) social ostracism of European families who became domiciled in India, even though they were fair-skinned and claimed pure European descent. This group is now designated as Domiciled European and undoubtedly includes fair Eurasians who can pass as Europeans; this is shown by the high percentage of Blood Group B reported by Greval (1940) among European patients in Calcutta.

The large British mercantile firms now frown upon marriage by their junior clerks with Domiciled Europeans or Anglo-

Indians. If they persist and get married, the young men may lose their jobs, or be passed over when it comes to promotion. If, however, a European man marries an educated Anglo-Indian, not too dark, and then succeeds in business, his children are usually classed as Europeans and can intermarry freely with the children of "pukka" (pure) Europeans. In this way Indian blood continues to filter into British families. In England Anglo-Indians are given European status.

Like nearly all communities in India, social or racial, the Anglo-Indians are an endogamous caste—a Christian group which follows European dress and customs to the best of its ability. The Anglo-Indians numbered under 140,000 at the 1931 Census. There are nowadays only a few accretions of F_1 individuals chiefly from tea-planting regions. These children are usually educated in special schools and then take their places among the Anglo-Indians. Retired British soldiers and other Europeans in minor positions often marry Anglo-Indian girls and settle down in India. Their children may try to be recognized as Domiciled Europeans, but they usually marry Anglo-Indians. Among 115 Anglo-Indian soldiers whose bloods were taken near Calcutta in 1941, 20 claimed British or Irish fathers and 10 had European mothers born in Europe. All the rest of the men had both parents Anglo-Indian.

ANGLO-INDIAN MATERIAL AND RESULTS

Bloods were grouped from 210 Anglo-Indians in the Calcutta area in the summer of 1941. These were from troops (mostly born in Bengal), orphan girls at Entally Convent and some nurses in the city hospitals. A good sample of over 300 Anglo-Indian bloods has also been grouped recently by Greval (1940) from hospital patients in Calcutta. The two samples were grouped by identical methods and differ chiefly with respect to Groups O and A, the groups in which the European ancestral strains involved also differ considerably. The results are both given in Table I.

TABLE I
BLOOD GROUP DISTRIBUTION AND FREQUENCIES IN ANGLO-INDIANS

Author	Nos.	Percentages in group				Frequency of			
		O	A	B	AB	p	q	r	D/ σ
Macfarlane	210	42.4	29.5	22.8	5.3	.197	.156	.651	1.2
Greval and Chandra ..	346	37.5	37.8	19.3	5.4	.255	.142	.608	1.7

The characteristic blood group distributions of India and of Western Europe are sharply contrasted, particularly with respect to the amount of Group B, which is four to five times more frequent in India than in Europe. Because caste in India has forced the F_1 persons from European-Indian crossings to become an endogamous community for generations, the F_1 blood group distribution should therefore be maintained.

Even though one may judge that the Anglo-Indians have a very mixed descent, a little investigation will show that a fairly good estimate can be obtained of the blood group ratios that have been involved in the racial mixture. The situation is not as simple as that studied by Boyd (1939b) in relation to the blood groups of European-American Indian crossings. Following Boyd's method, however, the blood group distributions of the five European stocks which have chiefly entered into the Anglo-Indians are listed in Table II, together with the gene frequencies; all data were taken from Boyd's tables (1939a). It will be observed that over 86 per cent. of the Dutch, English, Portuguese and Scottish belong to Groups O and A; although the French show more of Group B than the other four, all of them have a frequency of B (q) below 0.10. In Table III Indian blood group data are given for mixed (chiefly lower-caste) populations from Madras in the south (Tamils), Goa in the west (Mahrattas) and from Bengal in the northeast; these figures are taken from my compilation of Indian data (Macfarlane, 1938). Madras, Goa and Bengal are the regions in which most racial crossing has probably taken place. The three Indian samples show very similar blood group distributions with only 53 to 61 per cent. in Groups O and A together; all have more of Group B than of Group A and a frequency of B (q) of over 0.22.

TABLE II

BLOOD GROUP DATA FROM MIXED EUROPEAN POPULATIONS OF:
1. PORTUGUESE SOLDIERS; 2. DUTCH STUDENTS; 3. FRENCH AT PARIS; 4. SCOTTISH AT GLASGOW; 5. ENGLISH FROM EASTERN COUNTIES

Author	Nos. tested	Percentages in group				Gene frequencies		
		O	A	B	AB	p	q	r
1. Seiros da Cunha ...	459	38.4	52.5	6.1	3.0	.334	.047	.620
2. Herwerden and Boele-Nijland ...	3,085	45.7	41.2	9.6	3.5	.256	.068	.677
3. Dujarric and Kossowitch	1,265	39.8	42.3	11.8	6.1	.276	.088	.623
4. Matta	746	49.6	36.6	9.5	4.3	.224	.065	.704
5. Penrose and Penrose	1,000	43.2	47.7	6.4	2.7	.295	.048	.658

TABLE III

BLOOD GROUP DATA FROM MIXED INDIAN POPULATIONS IN :
1. NON-CASTE HINDUS, BENGAL ; 2. MAHRATTAS, GOA ; 3. TAMILS,
MADRAS AND CEYLON

Author	Nos. tested	Percentages in group				Gene frequency		
		O	A	B	AB	p	q	r
1. Macfarlane	320	30.9	22.2	40.0	6.9	.165	.279	.556
2. Correla	400	29.3	26.7	34.0	10.0	.207	.253	.540
3. Bals and Verhoef...	348	37.9	23.0	31.6	7.5	.166	.220	.615

The average blood group distributions and gene frequencies for the Europeans in Table II and for the Indians in Table III are given in Table IV. From these the expected F_1 distribution is obtained of O=38 per cent., A=34 per cent., B=22 per cent., AB=6 per cent. The average distribution in Anglo-Indians from the two samples in Table I is: O=39.8 per cent., A=33.8 per cent., B=21.1 per cent., AB=5.3 per cent. (see Table IV), which is very close to the above expected F_1 distribution. The average gene frequencies of the Calcutta Anglo-Indians also resemble closely those expected in an F_1 between the races involved.

TABLE IV

AVERAGES OF THE DATA IN TABLES II AND III WITH THE EXPECTED F_1 VALUES FROM A CROSS BETWEEN THEM COMPARED WITH THE ANGLO-INDIAN AVERAGES FROM TABLE I

	Percentages in group				Gene frequencies		
	O	A	B	AB	p	q	r
Indian average	32.7	24.0	35.2	8.1	.179	.251	.570
W. European average	43.4	44.1	8.7	3.8	.279	.064	.657
Expected F_1	38.0	34.0	22.0	6.0	.229	.157	.614
Anglo-Indian average	39.8	33.8	21.1	5.3	.227	.149	.625

Although the above calculations of the ancestral gene frequencies are necessarily only rough estimates, there is good evidence in support of the assertion that the Eurasians in India have maintained an F_1 condition for the past three or four centuries in spite of occasional back-crossing to the European ancestral stock.

Sub-group A_2 was found only twice in the 210 Anglo-Indian bloods. It was found in nearly 3 per cent. of the general Indian population of Calcutta (Macfarlane, 1939) and is still more frequent in the British.

There was opportunity only to test 65 of the Anglo-Indian bloods with some anti-M serum. Only 4 in 65 gave no reaction

and therefore belonged to Type N. The average for Indians in Calcutta is 11 per cent. Type N (Macfarlane, 1939). More tests are needed to elucidate the distribution of the blood types in Eurasians.

PARSEE BLOOD GROUPS

The Parsees are a community of Iranian descent who came to Bombay from Persia to escape Islamic persecution over ten centuries ago. They also are almost completely endogamous, but I was informed that originally some women were taken by Parsee men from the natives of Gujerat. The few pure Iranians among them, more recent arrivals in India, tend to look down upon the Parsees as "not pure bred."

The distribution of the blood groups was found in a small sample of one hundred. The community is small in Calcutta and was contacted in 1941 through the kind cooperation of Dr. B. S. Guha, of the Indian Museum, who is making an anthropometric study of the Parsees. They are an enterprising community of business people and they have a high standard of education. These Parsees appear to have a Near Eastern or Levantine type of blood group distribution similar to that found in some Arabs, in Syrians and Armenians. In Table V the Parsee blood group distribution is compared with those of Bengali Brahmins (the highest caste in Bengal) and with some data from near their original home to the west. The sample from Iranians at Samarkand shows a high percentage of Group B, it also runs this high in some Arabs where the amount of Group B shows considerable variation (Boyd, 1939a). It is hoped that

TABLE V
BLOOD GROUP DISTRIBUTION IN PARSEES, CALCUTTA, COMPARED WITH BENGALI BRAHMINS AND TWO NEAR EASTERN POPULATIONS

Community and author	Nos.	Percentages in group				Frequencies			
		O	A	B	AB	p	q	r	D/σ
Parsees (Macfarlane)	100	43	33	18	6	.216	.125	.656	0.7
Brahmins, Bengal (Grevil)	201	37.8	19.9	35.3	6.9	.145	.240	.615	0
Bedouin,* Mosul (Macfarlane)	206	43.7	31.1	16.5	8.7	.204	.115	.661	0.7
Iranians,* Samarkand (Libman)	500	30.6	31.8	31.6	6.0	.237	.235	.553	2.59

* Data from Boyd's Tables, 1939.

more data will shortly be obtained from the Parsees, for they seem to present a nice demonstration of a "racial island" of blood group distribution.

ACKNOWLEDGMENT

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SUMMARY

1. The racial and historic origins of the Eurasians in India, an endogamous community now called Anglo-Indians, are outlined.

2. The blood group distribution in 210 Anglo-Indians in Calcutta was: O = 42.4 per cent., A = 29.5 per cent., B = 22.8 per cent., AB = 5.3 per cent.

3. It is demonstrated that endogamy among these Eurasians has maintained an expected F_1 blood group distribution between a Portuguese, Dutch, French and British mixture on one side and lower caste Hindu strains from west, south and eastern India on the other.

4. Only two sub-group A_2 bloods were found in 210 Anglo-Indian bloods and only 4 type N bloods were found in 65 tested.

5. One hundred Parsees in Calcutta showed only 18 Group B bloods. They seem to form a racial island of a Near Eastern type of blood group distribution.

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LITERATURE CITED

Boyd, W. C.

1939a. *Tabulae Biologicae*, 17: 113-240.

1939b. *Am. Jour. Phys. Anthropol.*, 25: 215-235.

Greval, S. D. S., and S. N. Chandra

1940. *Indian Jour. Med. Res.*, 27: 1109-1116.

Love, H. D.

1913. "Vestiges of Old Madras." London.

Macfarlane, E. W. E.

1938. *Jour. Genetics*, 36: 225-237.

1939. *Jour. Roy. Asiatic Soc. Bengal, Science*, 5: 71-86.

DIFFERENTIAL SELECTION OF VARIANT JUVENILE SNAKES

DR. E. R. DUNN (1942) has recently pointed out that the scutellation in juvenile snakes tends to be more variable than that in adults. He shows that the reduction in variability is due to the death of certain abnormal juveniles. He regards many features of scutellation as adaptive, and draws the inference that these anomalies of scutellation may be, in some cases, the direct cause for the selection operating against the individuals in question. In other cases, an anomalous character may be correlated with other characters of negative value to the species.

I have tested these principles by examination of certain features of the scutellation of *Opheodrys vernalis* Harlan. A collection, in Field Museum, made by the late F. J. W. Schmidt and data contained in a paper on the smooth green snake by Grobman (1941) form the basis of the present study. The Schmidt collection consists of 21 adults and 32 juveniles (specimens measuring less than 200 mm) all from Clark County, Wisconsin. Acknowledgment is made to Mr. Karl P. Schmidt, who suggested further study of this problem, and to Mr. Clifford H. Pope, for their advice and criticism and for the use of laboratory space and collections in Field Museum of Natural History.

Table 1 compares the infralabials of the specimens listed by Grobman and of those in the Schmidt series. Grobman's data do

TABLE 1

	Grobman's sample	Schmidt collection	
		Adults	Juveniles
Number of specimens	1431	21	32
Mean	$7.80 \pm .013$	$7.86 \pm .078$	$7.47 \pm .076$
Standard deviation514	.505	.608
Coefficient of variability	6.59 per cent.	6.42 per cent.	8.13 per cent.

not indicate size or age of his specimens. I assume that the number of juveniles in his sample is much smaller than the number of adults as the above figures derived from Grobman's data approach those of the Schmidt collection adults very closely. The larger mean of the adult sample in the Schmidt series indicates that relatively fewer adult specimens than juveniles have a low number of infralabials.

The fusion of the loreal with the nasal affords another anomaly available for analysis. Grobman finds that the loreal and nasal

have fused in 12.7 per cent. of 1,445 specimens unsorted for age. In the Schmidt series the loreal is fused with the nasal in 9.5 per cent. of the adults and in 43.7 per cent. of the juveniles.

Since both fusion of the loreal and nasal and reduction in the number of labials are correlated with shortening of the head, it appears that selection operates against those individuals with small heads.

Four of the juvenile specimens in the Schmidt collection have one to five caudals single, whereas none of the adults show this abnormal condition.

One of the adults in the Schmidt collection has the loreal fused with the nasal; this specimen was the mother of a brood of four among which three exhibit the same character. This compares with the case reported by Dunn (1915) and supports his belief that such variation in the scales is hereditary.

These differences between the juvenile and adult populations tend to corroborate Dunn's statement concerning the correlation between the adaptive value of certain features of scutellation and their selection. They obviously corroborate the fact of negative selection of the more extreme variants in juvenile snakes.

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LITERATURE CITED

Dunn, E. R.

1915. *Proc. Biol. Soc. Wash.*, 28: 61-68.

1942. *Am. Nat.*, 76: 104-109.

Grobman, A. B.

1941. *Misc. Publ. Mus. of Zool., Univ. of Mich.*, No. 50: 1-38.

